Article

A species-level revision of the North American brontotheres *Eotitanops* and *Palaeosyops* (Mammalia, Perissodactyla)

BRYN J. MADER

Department of Biological Sciences and Geology, Queensborough Community College, 222-05 56th Avenue, Bayside, NY, 11364-1497.
Long Island Natural History Museum, P.O. Box 262, Levittown, NY, 11756. E-mail: bmader@qcc.cuny.edu

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Abstract

A systematic revision based on a morphological and statistical analysis recognizes two species of *Eotitanops* (*E. borealis*, and *E. gregoryi*) and three species of *Palaeosyops* (*P. paludosus*, *P. fontinalis*, and *P. robustus*) as valid. The name *P. robustus* is selected as having priority over the name *P. laticeps* under the Principle of First Reviser. *Eotitanops* is the only member of the subfamily Eotitanopinae and *Palaeosyops* is the only member of the subfamily Palaeosyopinae.

Key words: titanothere, Brontotheriidae, Eocene, Bridgerian, Gardnerbuttean, Blacksforkian, Twinbuttean, Bridger Formation, Washakie Formation, Huerfano Formation, Wind River Formation

Introduction

Mader (1989; 1998) published two major revisions of North American brontothere genera, the first significant works on this subject since Osborn's impressive, but flawed, treatment in 1929. In the 1998 paper, Mader included lists of valid species among the genera that he recognized, and referred readers to his unpublished doctoral dissertation for his justifications for the validity of these species. Recently, Mader (2008) presented a

formal revision of Bridgerian and Uintan brontothere species exclusive of *Palaeosyops*, including a full rationale for his species-level taxonomy.

The species-level revision of *Palaeosyops* and *Eotitanops* presented here, together with Mader (2008), completes a full systematic revision of all North American "paleobrontotheres" (see Schoch & Lucas 1985 or Mader 1989 for definition). In 2000, Gunnell and Yarborough also revised *Eotitanops* and *Palaeosyops* with similar conclusions to those presented here. Differences between the results of Gunnell and Yarborough and those reported here are discussed in the paper and are summarized in the Conclusions section. The fairly comprehensive revision of brontotheres recently published by Mihlbachler (2008) does not present a systematic revision of *Eotitanops* or *Palaeosyops*.

Eotitanops and *Palaeosyops* are plesiomorphic relative to all other brontotheres in that wear on the paracones and metacones is fairly direct while in other brontotheres wear is concentrated along the lingual edge of the ectoloph (Mader 1998). Furthermore, all other brontotheres have a distinct facial concavity near the junction of the frontal, nasal, and maxillary bones, whereas *Palaeosyops* and (probably) *Eotitanops* do not (see cladogram in Mader 1998, Fig. 36.5)

Abbreviations

Institutional. ACM, Pratt Museum, Amherst College, Amherst; **AMNH**, American Museum of Natural History, New York; **ANSP**, Academy of Natural Sciences of Philadelphia, Philadelphia; **UCM**, University of Colorado Museum, Boulder; **UCMP**, Museum of Paleontology, University of California, Berkely; **UM**, Museum of Paleontology, University of Michigan, Ann Arbor; **USNM,** United States National Museum, Smithsonian Institution, Washington, D. C.; **UW,** Geological Museum, University of Wyoming, Laramie; **YPM,** Peabody Museum of Natural History, Yale University, New Haven; **YPM-PU**, Princeton University Collection, Peabody Museum of Natural History, Yale University, New Haven.

Statistical. DF, degrees of freedom; **n**, number of cases in sample; **s**, standard deviation of sample; **V**, coefficient of variation.

Methods

The methods outlined here follow Mader (2008), and the reader should read that paper for a more extensive discussion of the reasoning behind various analytical choices:

1. The present study focuses primarily on cranial and upper dental morphology and measurements because most brontothere types consist of cranial or upper dental material and because skulls are rarely found in association with jaws or postcranial elements.

2. The systematic conclusions presented in this paper are primarily the result of morphological analysis in which the presence of shared derived characters is the major criterion for the recognition of taxa.

3. Specimens were sorted into several morphologically homogeneous groups that could not be subdivided further on the basis of their anatomy. These groups were recognized as genera by Mader (1989). It is assumed that these groups may contain more than a single species, which might be delineated through analysis of their size.

4. Measurements were taken in millimeters following the method of Osborn (1929, Fig. 255).

5. To prevent the maturity of the specimens from having an influence on the results, only specimens with adult dentitions (M3 fully erupted) were used.

6. The effects of deformation on skull size and the size of the cheek tooth series were minimized by averaging the left and right sides of the same specimen whenever possible. If only one side was preserved, however, then the available measurement was used unless deformation was deemed to be so extreme as to make the measurement inaccurate. Average values for left and right sides were not calculated for individual tooth measurements.

7. Estimated values were generally avoided. In cases where the defect in a structure was minor (such as a small chip of enamel missing from the surface of a tooth) an estimated measurement was taken, but only if the

uncertainty involved in making the estimate was exceedingly small (≤ 1mm for tooth measurements and a few millimeters for tooth row or skull length measurements). The size of the defect was itself evaluated by comparison to surrounding intact structures.

8. Cluster analyses employed Euclidean distance as the distance metric and nearest neighbor (single linkage) as the method of linkage. Groups generated by cluster analysis were not automatically assumed to represent different taxa as they might be different size groups within a single species (such as males and females, juveniles and adults, or coincidental groupings).

9. In general, the criteria of Simpson *et al.* (1960) were employed in evaluating the coefficient of variation. Individual values for the coefficient between 4 and 10 were considered typical of a single species. Values below 4 were taken to indicate that the sample size is probably too small to show the true variability or, in the case of analyzing groups delineated by cluster analysis, variation inconsistent with a single species. Values above 10 were taken to indicate that the sample is probably not homogeneous and may consist of more than one taxon. An average value of V was also calculated and was expected to range between 5 and 7 for a single species.

10. *T*-tests were used to compare groups that were from different stratigraphic levels or delineated by cluster analysis. F-tests were employed first to confirm that group variances were equal and, if not, Welch's *t'* (*t*-test with separate variances) was used instead of a standard *t*-test. If the size of one of the groups consisted of fewer than ten cases (the usual situation in brontothere samples) then Box's approximation of F for small samples was employed.

11. It is assumed that at least some *t*-test results will suggest that a significant difference exists where there is none (Type I error). The formula $1-(1-\alpha)^k$ was used to calculate the likelihood of such an event occurring at least once in a group of tests, where α is the probability used per individual test (.05 for these analyses) and k is the number of *t*-tests performed.

12. It is deemed that a Bonferroni Correction is not appropriate for the *t*-tests appearing in this study and would result in an over-abundance of Type II errors.

Because specimens of *Eotitanops* tend to be very fragmentary, and estimated measurements were avoided, it was not possible to compile a database of sufficient size for this genus. A provisional analysis was performed, however, using partially estimated data (including lower jaw measurements) from Osborn (1929). An analysis of specimens referred to *E. minimus* (a junior synonym of *E. gregoryi* in the present paper) was based on lower molar data appearing in Robinson (1966).

Revision of plesiomorphic North American brontothere genera

Order PERISSODACTYLA Owen 1848

Family BRONTOTHERIIDAE Marsh 1873

Discussion: Mader (1989; 1998) divided the Brontotheriidae into two relatively large monophyletic subfamilies: the Dolichorhininae and the Brontotheriinae (= Telmatheriinae, sensu Mader 1989). *Eotitanops* and *Palaeosyops* were resolved as sister genera to these subfamilies, but were not found to comprise a monophyletic taxon. Recent phylogenetic analyses by Mihlbachler (2008) generally support this conclusion. *Eotitanops* and *Palaeosyops* are accorded their own subfamilies in the present revision.

Subfamily EOTITANOPINAE Osborn 1914

Included genera: *Eotitanops*
   Diagnosis: Same as for member genus, *Eotitanops* (see below). Sister taxon to all other brontothere subfamilies (see cladogram in Mader 1998, Fig. 36.5)

Genus *EOTITANOPS* Osborn 1907

Age: Early Bridgerian.
    Subage: Gardnerbuttean.
    Type species: *E. borealis* (Cope 1880).
    Included species: *E. gregoryi* Osborn 1913 (= *E. minimus* Osborn 1919).
    Diagnosis: Small-sized (average length P2 to M3 is 91 mm in AMNH 14887) brontothere with a well developed upper canine; long upper and lower diastema; unmolarized premolars; relatively large paraconules; and hypocone or pseudohypocone variably present on M3. *Eotitanops* is probably distinguished from all other brontotheres by its relatively long face, a plesiomorphic character state that is similar to outgroup perissodactyls. There are no synapomorphies that distinguish *Eotitanops* from other brontotheres (although all other brontotheres have synapomorphies that distinguish them from *Eotitanops*).

    Discussion: In 1880 Cope described a maxilla fragment of a small brontothere (AMNH 4892) from the Wind River Basin as a new species of *Palaeosyops*, *P. borealis*. Osborn (1897) included *P. borealis* in the genus "*Telmatotherium*" (*T. boreale*) but later concluded that it was an entirely new genus, which he named *Eotitanops*. Osborn first used this new generic name in 1907 but did not formally diagnose the genus until 1908.

    In 1929 Osborn gave the following diagnosis for *Eotitanops borealis* (comparisons are against *E. gregoryi* and *E. brownianus*, both discussed below):

> "Of larger size, p2–m3 94–98 millimeters; premolar teeth more complicated, as shown in neotype and associated specimens; p2 with very rudimentary paraconid and metastylid; P2–4 with progressively developing tritocones [= metacones] and single internal deuterocones [= protocones] backwardly inclined, crowns subtriangular; M1–3 with distinct protoconules [= paraconules]."

    The "neotype" mentioned by Osborn is a fragmentary skull (AMNH 14887, Figure 1) and jaws. Despite its poor condition the skull is the most complete cranial remains of *Eotitanops* known. Osborn designated this specimen as the neotype of *E. borealis* in 1929, but because the original type (AMNH 4892) is still preserved, Osborn's specimen has no nomenclatural significance (Article 75, International Code of Zoological Nomenclature, Ride *et al*. 1999). It is merely a referred specimen.

    In 1881 Cope described a partial lower jaw (AMNH 4885) from the Wind River Basin, which he identified as a new species of *Lambdotherium* and named *L. brownianum* (Cope 1881). Osborn (1929), however, correctly recognized that this jaw is actually a specimen of *Eotitanops*. Osborn accepted *E. brownianus* (note the emendation of the trivial name) as a valid species and distinguished it from the other species of *Eotitanops* that he recognized by its relatively small size and simplicity of the premolars.

    Expeditions from the American Museum of Natural History collected from the Wind River Basin in 1891 and between 1909 and 1911. In 1913 Osborn wrote a paper based on the material collected by these expeditions in which he named three new species of *Eotitanops*: *E. gregoryi*, *E. princeps*, and *E. major*.

    Eotitanops gregoryi was based on an incomplete lower jaw with some of the right cheek dentition intact and fragments of the left maxilla containing M2 and M3 (AMNH 14889). Osborn (1913) gave the following diagnosis of the taxon:

> "Of inferior size. p2 – m3 = [78.4 mm]; m1–3 = [49]; p2–3 with the internal cusps, paraconid and metaconid, consisting of rectigradations of most rudimentary stage; hypoconulid of m3 very small; M3 with a single internal cone, no hypocone".

    Measurements in the above diagnosis appearing in brackets were originally reported by Osborn in meters, but have been converted here to millimeters. The term "rectigradation" refers to newly evolved morphological characters upon which the taxon could be defined. In 1929 (p. 291) Osborn repeated the above diagnosis almost verbatim and went on to add that the "primitiveness" of the species is apparent when the p3 is

compared to that of *Eotitanops borealis* and *E. princeps*. According to Osborn, the p3 of *E. gregoryi* is laterally compressed; the hypoconid is distinct; and the paraconid, metaconid, and entoconid are all in an extremely rudimentary state. Osborn also stated that the p2 is plesiomorphic, being short and compressed with a very rudimentary hypoconid, and that the molars are plesiomorphic as well. According to Osborn the metastylid and entostylid of the molars are extremely rudimentary and the hypoconulid of the m3 is small, subconic, and externally (= buccally) located.
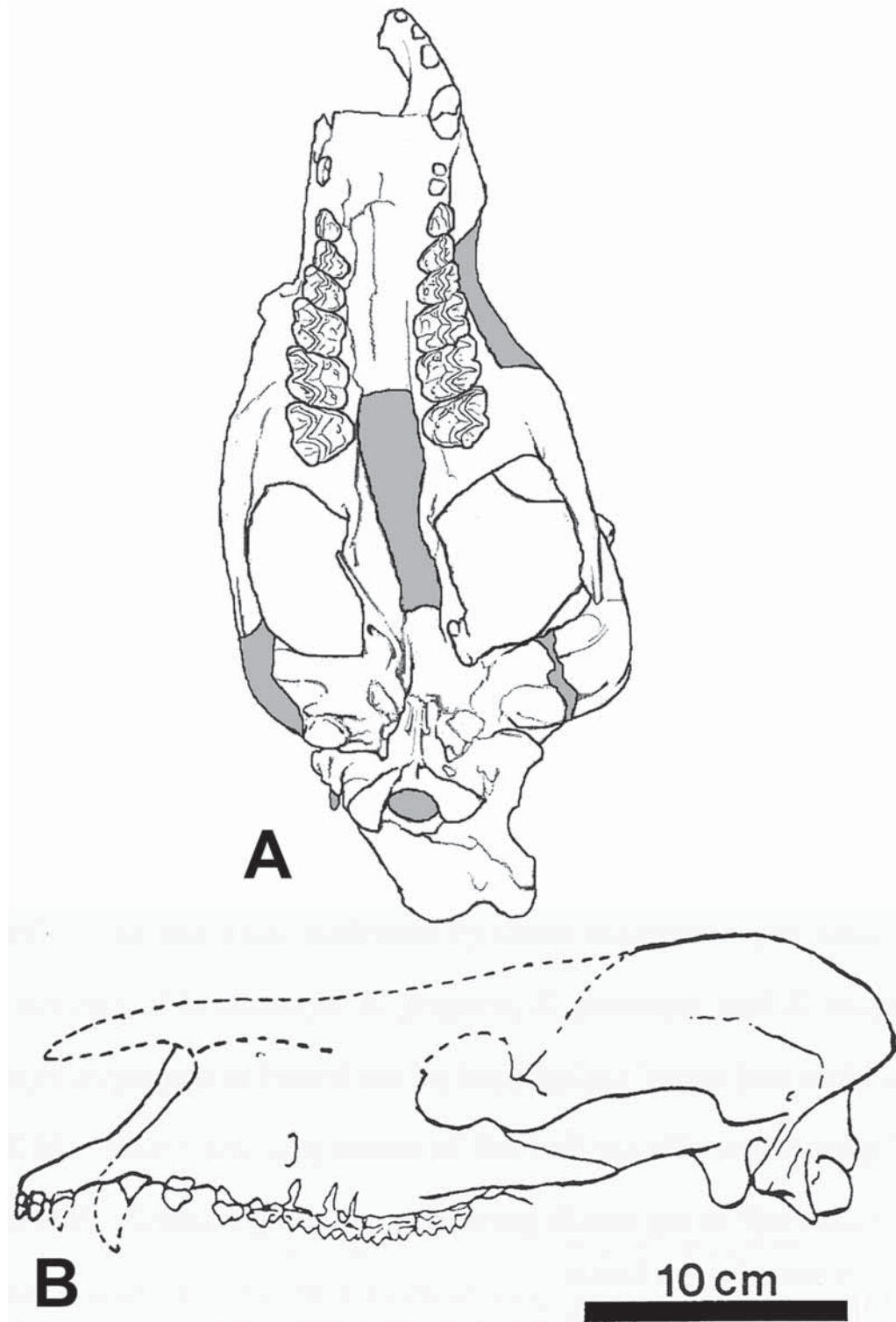

FIGURE 1. Skull of *Eotitanops borealis* (AMNH 14887, Osborn's "neotype") in **A**, ventral, and **B**, lateral view. After Osborn (1929).

Eotitanops princeps was based on a lower jaw and partial postcranial skeleton (AMNH 296) that had been originally referred to *Palaeosyops borealis* by Osborn and Wortman (1892). This specimen, although very incomplete, is the most complete skeleton of *Eotitanops* known. In 1913 Osborn concluded that this specimen represented a new species of *Eotitanops* and cited the following as diagnostic characters (all comparisons are against *E. gregoryi*, *E. brownianus*, and *E. borealis*):

"Of still larger size, p2–m3 [105 mm (estimated)]. Inferior premolar teeth somewhat more complicated, as shown in the type specimen. p2 with elevated, distinct, but very rudimentary paraconid and metaconid; entoconid very rudimentary; talonid narrow. p3, paraconid quite distinct, elevated; metaconid small, distinct; entoconid rudimentary; talonid broad. p4, talonid broad; entoconid distinct. Hypoconulid of m3 rounded, more robust. Ramus larger and more robust.
The more advanced development of the premolar rectigradations, the increased size of the teeth and of the jaw, the larger size of the hind feet in the referred specimen (Am. Mus. 4902) [= AMNH 4902] combine to distinguish this specimen as a mutation or subspecific stage between *E. borealis* and *E. major*."

In 1929 Osborn stated that *Eotitanops princeps* is a valid specific stage of *Eotitanops* (p. 193) but elsewhere (p. 295) repeated his earlier statement (1913) that *E. princeps* is a subspecific stage between *E. borealis* and *E. major*. In 1929 Osborn repeated his previously published diagnosis for *E. princeps* (1913) almost word for word but made some important modifications. In the 1929 diagnosis Osborn stated that the metastylid of p2 and p3 is rudimentary or small rather than the metaconid, added that the p2 entoconid is rudimentary if present, stated that the entoconid shelf of p4 is distinct (rather than the entoconid itself), and added the observation that the p4 is submolariform.

Eotitanops major was based on a left median metatarsal (metatarsal III) and the distal end of a tibia (AMNH 14894). Osborn (1913) characterized the species as "ill-defined" and distinguished from other species of *Eotitanops* by its supposedly larger size. In 1929 Osborn again recognized *E. major* as a valid species.

To facilitate comparison of Osborn's diagnoses I have compiled in tabular form most of the characters that Osborn used to define the Wind River species of *Eotitanops* for which there was dental material available (Table 1). All of the characters that Osborn used in the diagnosis of more than one species are included in the table, but I have omitted some of the characters that Osborn used in the diagnosis of only a single species.

Most of the characters listed in Table 1 show no appreciable differences between taxa. For example, the descriptions of the p2 paraconid as being "very rudimentary" (*Eotitanops princeps* and *E. borealis*), "very low on crown" (*E. brownianus*), and "extremely rudimentary" (*E. gregoryi*), do not imply any significant difference among the taxa. Similarly, descriptions of the p2 entoconid as being "very rudimentary" (*E. princeps* and *E. borealis*) or "invisible" (= absent?, *E. brownianus*) do not suggest an important difference.

The only characters showing significant differences between two or more of the taxa are the morphology of the p2 hypoconid, p3 paraconid, and m3 hypoconulid. The p2 hypoconid is described as "distinct and elevated" in *Eotitanops brownianus* but "very rudimentary" in *E. gregoryi*. The p2 hypoconid on the type of *E. brownianus* is not particularly distinct or elevated, however, and the entire p2 talonid region is lacking in the type of *E. gregoryi*. Although Osborn's observation cannot be confirmed, the weak development of the p2 hypoconid in *E. brownianus* suggests that this difference is insignificant.

The p3 paraconid of *Eotitanops princeps* is described as "quite distinct and elevated" while that of *E. gregoryi* is "very rudimentary". Although the p3 paraconid of *E. princeps* is slightly more distinct than that of *E. gregoryi*, the p3 paraconid of *E. princeps* is actually rather poorly developed and, as Wallace (1980) pointed out, is hardly more prominent than the p3 paraconid of AMNH 14888, which Osborn (1929) referred to *E. borealis*. The small size of the p3 paraconid in the type of *E. gregoryi* might be diagnostic for the species, but the character variability cannot be assessed without additional material.

Finally, the m3 hypoconulid of *Eotitanops princeps* is described as "robust and rounded", that of *E. borealis* as "small and lophoid", and that of *E. gregoryi* as "very small and subconic". The m3 hypoconulid of

E. borealis is further described as being "centrally positioned" while that of *E. gregoryi* is "positioned externally" (that is, buccally). The m3 hypoconulid on the type of *E. gregoryi* is actually very similar morphologically to that of AMNH 14888, which Osborn referred to *E. borealis*, and not more buccally positioned. Although the m3 hypoconulid on the type of *E. princeps* is very large and rounded, the significance of this character is unknown. As noted by Wallace (1980), the distal part of the brontothere tooth row is highly variable and the size and morphology of the M3 hypocone or m3 hypoconulid generally make poor diagnostic characters.

TABLE 1. Characters used by Osborn (1929) to distinguish the four species of *Eotitanops* from the Wind River Basin for which dental material was known.

Character	*E. princeps*	*E. brownianus*	*E. borealis*	*E. gregoryi*
p2 shape	———	Compressed	———	Short, compressed
p2 paraconid	Elevated and distinct	Very low on crown	Very rudimentary	Extremely
p2 metastylid	Elevated and distinct	Rudimentary	Very rudimentary	———
p2 talonid	narrow	———	———	———
p2 entoconid	Very rudimentary	Invisible	Very rudimentary	———
p2 hypoconid	———	Distinct and elevated	———	Very rudimentary
p3 paraconid	Quite distinct and	———	———	Extremely
p3 metastylid	Small but distinct	———	———	———
p3 talonid	Broad	———	———	———
p3 entoconid	Rudimentary	———	———	Extremely
p4 talonid	Broad	———	———	———
p4 entoconid	Distinct	———	———	———
m3 hypoconulid	Robust and rounded	———	Small, sublophoid,	Very small,

Thus, based on the morphology as described by Osborn there does not appear to be any significant differences between the taxa that he recognized. It is still possible, however, that size differences may allow for the delineation of different species.

Unfortunately, most available specimens of *Eotitanops* are fragmentary, and because I have refrained from measuring specimens with any but the slightest of imperfections, I have not been able to compile a database of sufficient size to analyze statistically. Accepting the imprecision introduced by partially estimated measurements, however, then a provisional statistical analysis may be performed using measurements provided by Osborn (1929, p. 290) for several specimens of *Eotitanops*..

Table 2 presents the summary statistics for all of the specimens of *Eotitanops* for which Osborn (1929) provided data. Almost half of the individual values of V (rounded to the nearest whole number) are greater than 10, and the majority of the values of V between 4 and 10 are at the higher end of this range (>8). Finally, the average value of V for the sample is also very high (= 10.1). These results strongly suggest that the sample is heterogeneous and represents more than a single species. The types of three species (*E. brownianus*, *E. princeps*, and *E. gregoryi*) are included in the sample.

Cluster analysis of all of the variables listed in Table 2 produces a dendrogram (Figure 2) in which the type of *Eotitanops princeps* groups with specimens referred to *E. borealis* and the types of *E. gregoryi* and *E. brownianus* group out separately. The type of *E. brownianus* is very incomplete and Osborn only reported measurements for the length of the lower cheek tooth series (exclusive of p1), length of the premolar series (exclusive of p1), and the length of the molar series. Cluster analysis using only these three variables produces a dendrogram in which the type of *E. brownianus* groups with referred specimens of *E. borealis*, while the types of *E. princeps* and *E. gregoryi* group out separately (Figure 3).

TABLE 2. Summary statistics for specimens of *Eotitanops* from the Wind River Basin (data from Osborn 1929; all measurements in millimeters).

	n	Range	M	s	V
Length p2 to m3	6	78.0 – 105.0	93.5	±9.1	9.7
Length p2 to p4	6	29.4 – 39.0	35.6	±3.4	9.5
Length Lower Molar Series	6	49.0 – 66.0	57.8	±5.6	9.8
Length m3	5	19.5 – 25.0	22.5	±2.0	8.9
Width m3	3	10.7 – 14.0	12.1	±1.7	14.3
Length m2	4	15.5 – 21.0	18.4	±2.3	12.5
Width m2	4	10.5 – 14.0	12.3	±1.5	12.4
Length m1	4	14.5 – 18.3	16.2	±1.6	10.0
Width m1	4	8.5 – 12.0	10.4	±1.5	14.4
Length p4	3	12.0 – 13.0	12.5	±0.5	4.0
Width p4	3	7.5 – 8.0	7.8	±0.3	3.7
Length p3	4	9.5 – 12.5	11.5	±1.4	11.8
Width p3	4	5.2 – 7.0	6.3	±0.8	12.1
Length p2	4	8.8 – 13.0	11.3	±1.8	15.9
Width p2	4	6.0 – 6.3	6.1	±0.2	2.5
AVERAGE V					10.1

FIGURE 2. Cluster dendrogram for specimens of *Eotitanops* from the Wind River Basin resulting from a cluster analysis of all variables listed in Table 2 (based on data from Osborn 1929). **a**, type of *Eotitanops princeps*; **b**, type of *E. gregoryi*; **c**, type of *E. brownianus*.

Eotitanops brownianus is probably not a valid species. The type is morphologically similar to specimens of *E. borealis* and none of the characters cited by Osborn convincingly distinguish them. The three variables for which Osborn provided measurements for the type specimen (length p2 to m3, length p2 to p4, and length m1 to m3) are close to those of his referred specimens of *E. borealis* and it is likely that *E. brownianus* is a junior synonym of this taxon. Although Osborn did not indicate it, his measurements for *E. brownianus* must be estimated values because the type of *E. brownianus* is missing the crowns on all but the left second premolar, and, thus, the minor size differences cited between the two species cannot be accorded great significance.

Eotitanops princeps is also probably invalid, based on morphology and size considerations (see below), but *E. gregoryi* appears to be valid. In Figure 2 and especially in Figure 3, the type of *Eotitanops gregoryi* is well-separated from most other specimens of *Eotitanops* in the sample. This separation is accounted for by the extremely small size of the specimen. If the type of *E. princeps* (a rather large individual) is dropped from the statistical analysis so that the remaining specimens in the sample are closer in size to the type of *E. gregoryi*, the individual and average values of V for the sample remain high (Table 3). This result suggests that the type of *E. gregoryi* is largely responsible for the high individual and average values of V in the original statistical analysis (Table 2).
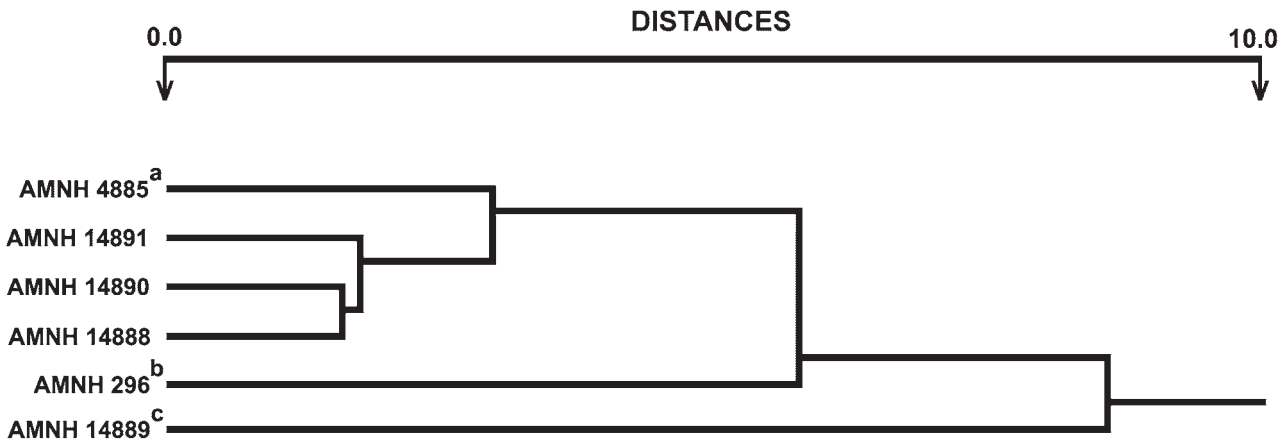

FIGURE 3. Cluster dendrogram for specimens of *Eotitanops* from the Wind River Basin resulting from a cluster analysis of length of the cheek tooth series (exclusive of p1), length of the premolar series (exclusive of p1), and length of the molar series (based on data from Osborn 1929). **a**, type of *Eotitanops brownianus*; **b**, type of *E. princeps*; **c**, type of *E. gregoryi*.

TABLE 3. Summary statistics for specimens of *Eotitanops* from the Wind River Basin exclusive of the type of *E. princeps* (data from Osborn 1929; all measurements in millimeters).

	n	Range	M	s	V
Length p2 to m3	5	78.0 – 98.0	91.2	±8.0	8.7
Length p2 to p4	5	29.4 – 38.0	34.9	±3.3	9.3
Length Lower Molar Series	5	49.0 – 60.0	56.2	±4.4	7.9
Length m3	4	19.5 – 23.2	21.9	±1.7	7.8
Width m3	2	10.7 – 11.5	11.1	±0.6	5.1
Length m2	3	15.5 – 19.0	17.5	±1.8	10.3
Width m2	3	10.5 – 13.0	11.7	±1.3	10.7
Length m1	3	14.5 – 16.3	15.4	±0.9	5.9
Width m1	3	8.5 – 11.0	9.8	±1.3	12.8
Length p4	3	12.0 – 13.0	12.5	±0.5	4.0
Width p4	3	7.5 – 8.0	7.8	±0.3	3.7
Length p3	3	9.5 – 12.0	11.2	±1.4	12.9
Width p3	3	5.2 – 7.0	6.2	±0.9	14.9
Length p2	3	8.8 – 12.0	10.8	±1.7	16.0
Width p2	3	6.0 – 6.2	6.1	±0.1	1.9
AVERAGE V					8.8

If the type of *Eotitanops gregoryi* is excluded from the statistical analysis, however, (and the type of *E. princeps* is retained) then all but three of the individual values of V (rounded to the nearest whole number) fall

within the range of 4 to 10 (Table 4). Two out of the three values of V that are outside of this range are below 4, which suggests that the samples from which these values were calculated may be too small to show all of the variation that is actually present. The average value of V for the sample exclusive of *E. gregoryi* is 6.36, which is within the ideal range suggested by Simpson *et al*. (1960). Thus, if the type of *E. gregoryi* is excluded from the analysis, the individual and average values of V for the specimens remaining in the sample are within the range accepted for a single species (Table 4). If *E. gregoryi* is included in the sample, however, then the individual and average values of V generally exceed the range established for a single species (Tables 2 and 3).

TABLE 4. Summary statistics for specimens of *Eotitanops* from the Wind River Basin exclusive of *E. gregoryi* (data from Osborn 1929; all measurements in millimeters).

	n	**Range**	**M**	**s**	**V**
Length p2 to m3	5	90.0 – 105.0	96.6	±5.6	5.8
Length p2 to p4	5	35.0 – 39.0	36.8	±1.6	4.5
Length Lower Molar Series	5	55.0 – 66.0	59.6	±4.0	6.8
Length m3	4	22.0 – 25.0	23.3	±1.3	5.4
Width m3	2	11.5 – 14.0	12.8	±1.8	13.9
Length m2	3	18.0 – 21.0	19.3	±1.5	7.9
Width m2	3	11.7 – 14.0	12.9	±1.2	8.9
Length m1	3	15.5 – 18.3	16.7	±1.4	8.6
Width m1	3	10.0 – 12.0	11.0	±1.0	9.1
Length p4	3	12.0 – 13.0	12.5	±0.5	4.0
Width p4	3	7.5 – 8.0	7.8	±0.3	3.7
Length p3	3	12.0 – 12.5	12.2	±0.3	2.4
Width p3	3	6.3 – 7.0	6.6	±0.4	5.5
Length p2	3	11.5 – 13.0	12.2	±0.8	6.3
Width p2	3	6.0 – 6.3	6.1	±0.2	2.8
AVERAGE V					6.4

Eotitanops gregoryi is therefore considered a valid species of *Eotitanops* distinguished from *E. borealis* primarily by its much smaller size. This conclusion is further supported by *t*-tests performed by Wallace (1980) in which the type of *E. gregoryi* separated out from other specimens of Wind River *Eotitanops* with a probability of greater that 95 % for most dental measurements.

The preceding statistical analyses suggest that *Eotitanops princeps* is a junior synonym of *E. borealis*. Although the type of *E. princeps* is the largest specimen of *Eotitanops* described to date, it is not so large that it must be recognized as a distinct species. Even though *E. princeps* groups out separately from most specimens of *Eotitanops* in a cluster analysis comparing the lengths of p2–m3, p2–p4, and m1–m3, *E. princeps* groups with referred specimens of *E. borealis* when all variables are considered. Analysis of the coefficient of variation demonstrates that the type of *E. princeps* and specimens referred to *E. borealis* all fall within the size range of a single extant mammalian species. While the large hypoconulid on the m3 of the type of *E. princeps* might be considered diagnostic, the documented variability of the distal brontothere tooth row renders this character suspect for diagnosis.

The fourth Wind River species of *Eotitanops* recognized by Osborn, *E. major*, was based upon a left median metatarsal (metatarsal III) and the distal end of a tibia. Osborn's main justification for the recognition of *E. major* as a valid species was its larger size compared to *E. princeps*. Although the type specimen of *E. princeps* does not have any postcranial material that can be directly compared to the type of *E. major*, Osborn referred a partial pes (AMNH 4902) to *E. princeps* that probably was the basis for his size comparison. Although the median metatarsal of this referred specimen is considerably smaller than that of the type of *E.*

major, neither size ranges nor the significance of size differences have been established for this element in *Eotitanops*. Accordingly, *E. major* is regarded as a junior synonym of *E. borealis*. If it is later be determined that *E. princeps* is a valid species, then *E. princeps* and *E. major* may be synonyms.

In 1919 Osborn described the lower cheek teeth (p2–m3, AMNH 17439) of a diminutive brontothere from the upper part of the Huerfano Formation (Huerfano B) as a new species of *Eotitanops*, *E. minimus* distinguished from *E. gregoryi* by its smaller size. In 1929 Osborn again recognized *E. minimus* as a valid species of *Eotitanops*, but did not provide a more complete diagnosis of the taxon.

Osborn (1929) also identified specimens of *E. gregoryi* (AMNH 17418) and *E. brownianus* (AMNH 17441) from the upper part of the Huerfano Formation, but Robinson (1966, p. 67) referred the specimen of *E. gregoryi* to *E. minimus* (apparently because it is smaller than *E. gregoryi* from the Wind River Basin) and identified the specimen of *E. brownianus* as having come from his locality VII, which is in the lower faunal zone (the part of the Garcia Canyon Local Fauna that is equivalent to the *Eotitanops borealis* Assemblage Zone in the Wind River Basin). In addition to AMNH 17418 and the type, Robinson identified two other specimens of *E. minimus*: AMNH 56539 and YPM 16439. According to Robinson, all four of these specimens are from his locality II, which is in the upper faunal zone of the Huerfano Formation (Gardnerbutte Local Fauna).

According to Osborn (1929), the discovery of a "dwarf titanothere" together with brontotheres of the same size as *Eotitanops gregoryi* and *E. brownianus* in the same geologic horizon "reveals the existence of what is probably a distinct phylum of diminutive titanotheres separable from the Eotitanopinae." Osborn was not willing, however, to formally recognize such a group until more complete skeletal material was available.

Wallace (1980) concluded that *Eotitanops minimus* represents an entirely new genus and provided the following diagnosis of the taxon:

"Small brontotheriid with relatively low, bunodont lower molar and premolar cusps; molar talonid basin broad and shallow and trigonid basin shallow, but relatively short anteroposteriorly; molar metalophid poorly developed and molar hypolophid absent; third lower molar hypoconulid reduced relative to other (earlier and later) brontotheriids, with cusp closely appressed to entoconid and having no lingual basin whatsoever; third upper molar with rudimentary or no metastylar ridge and no posterior cingulum; fourth lower premolar entoconid small, low, but distinct."

Of these characters, the presence of a distinct entoconid on p4, and possibly the size and morphology of the hypoconulid of m3, are likely synapomorphies.

Eotitanops minimus is most probably a junior synonym of *E. gregoryi*. Both *E. gregoryi* and *E. minimus* possess an entoconid on p4 (see Figure 4), and this may be a derived character as Wallace suggested. The presence of an entoconid on the p4 of *Phenacodus* (regarded as a sister taxon to perissodactyls), however, and on some specimens of *Hyracotherium* (basal Equidae?), raises some uncertainty about the polarity of this character. A limited statistical analysis also strongly suggests that *E. gregoryi* and *E. minimus* are similar in size (within the range of a single extant mammalian species), but are distinctly smaller than specimens of *E. borealis*.

Although I do not have numeric data for specimens of *Eotitanops minimus*, Robinson (1966, p. 67) provided measurements of the second lower molar for four specimens of *Eotitanops* from the Huerfano Formation (including the type of *E. minimus*) and four specimens of *Eotitanops* from the Wind River Formation. The Wind River sample consisted of three specimens of *E. borealis* and the type of *E. gregoryi*.

The coefficients of variation for the combined Wind River and Huerfano sample (Table 5) are very high (12 to 13, rounded to the nearest whole number), suggesting that the combined sample is not homogeneous and probably consists of more than a single taxon. Cluster analysis of all three variables in Table 5 results in a dendrogram (Figure 5) in which two size groups are clearly delineated. Specimens of *Eotitanops borealis* from the Wind River Formation form one size group and specimens of *E. minimus* from the Huerfano Formation form the other. Interestingly, although the type of *E. gregoryi* is from the Wind River Formation, it groups among the specimens of *E. minimus*.
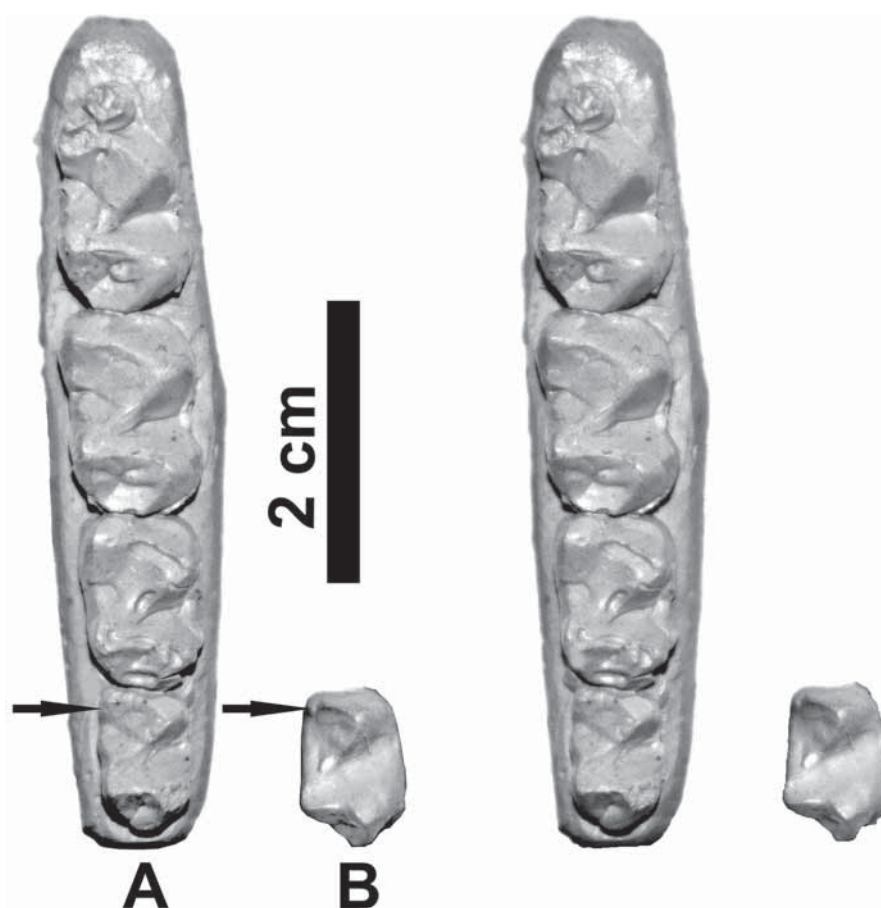
FIGURE 4. Stereophotographs of lower dentitions of *Eotitanops gregoryi*. **A**, AMNH 17439 (type of *E. minimus*, cast of p4–m3) and **B**, AMNH 11489 (type of *E. gregoryi*, cast of p4). Arrows point to entoconid on p4.

TABLE 5. Summary statistics for specimens of *Eotitanops* from the Wind River and Huerfano Basins (data from Robinson 1966; all measurements in millimeters).

	n	Range	M	s	V
Length m2	7	14.5 – 20.0	17.2	±2.1	12.2
Width m2 Trigonid	8	9.1 – 12.5	10.7	±1.4	12.7
Width m2 Talonid	8	9.3 – 12.5	10.9	±1.3	11.6

If the specimens of *Eotitanops borealis* are dropped from the analysis, and the coefficient of variation recalculated for the remaining individuals (the specimens of *E. minimus* and the type of *E. gregoryi*), then the resulting values of V are well within the parameters established for a single mammalian species (Table 6). Although this statistical analysis was based on size variation in a single tooth, it indicates that *E. gregoryi* and *E. minimus* are probable synonyms.

TABLE 6. Summary statistics for specimens of *Eotitanops* from the Wind River and Huerfano Basins exclusive of specimens of *E. borealis* (data from Robinson 1966; all measurements in millimeters).

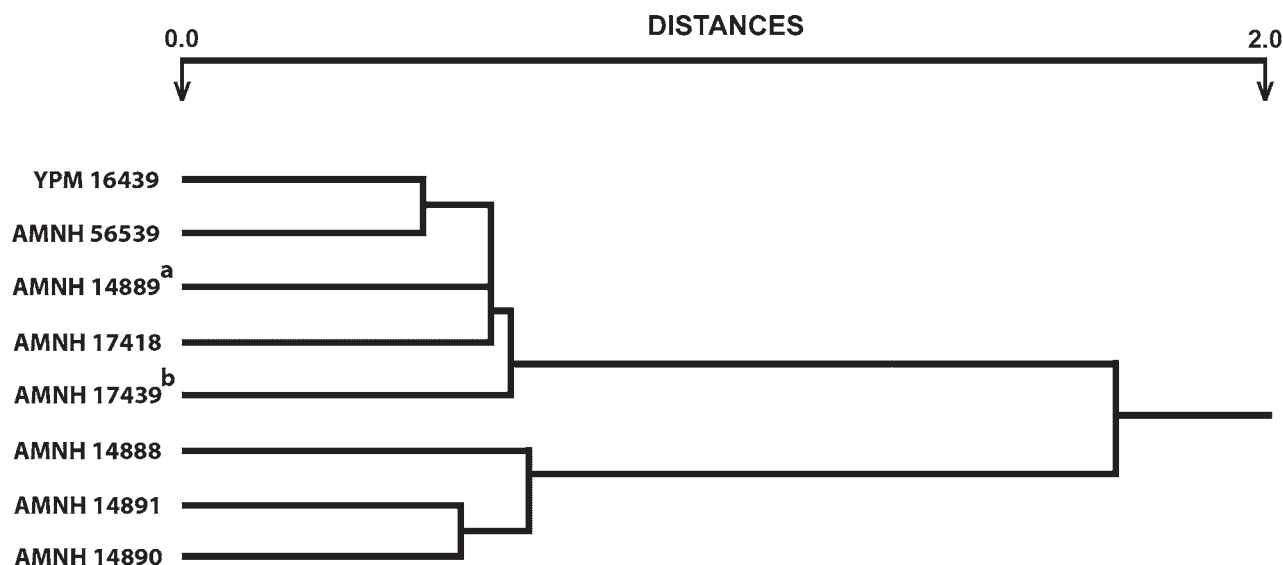|	n	Range	M	s	V
Length m2	4	14.5 – 17.0	15.7	±1.0	6.6
Width m2 Trigonid	5	9.1 – 10.6	9.8	±0.6	6.3
Width m2 Talonid	5	9.3 – 10.9	10.1	±0.6	5.8

FIGURE 5. Cluster dendrogram for specimens of *Eotitanops* from the Wind River and Huerfano Basins resulting from a cluster analysis of all three variables listed in Table 5 (based on data from Robinson 1966). **a**, type of *Eotitanops gregoryi*; **b**, type of *E. minimus*.

As noted above, Osborn (1929) suggested and Wallace (1980) concluded that the species *Eotitanops minimus* represents a new genus distinct from *Eotitanops*. Both writers, however, recognized *E. gregoryi* as a valid species of *Eotitanops*. Little is known about the morphology of *E. gregoryi* (= *E. minimus*), however, and it is difficult to demonstrate that it can be referred to *Eotitanops*, or conversely that is should be assigned to a new genus. Given that the lower dentition of "*Eotitanops*" *gregoryi* is similar to that of *E. borealis*, and that previous authors have recognized "*Eotitanops*" *gregoryi* as a species of *Eotitanops*, I provisionally accept this generic identification as correct. Alternatively *Eotitanops gregoryi* could be classified simply as a "primitive brontothere, *incertae sedis*" rather than attempting to make a definite generic assignment.

The conclusions regarding valid species of *Eotitanops* presented above are largely the same as those reached by Gunnell and Yarborough (2000). Both the present paper and Gunnell and Yarborough recognize a large form and a small form of *Eotitanops*, and both papers refer the large form to *E. borealis*. The small form is here referred to *E. gregoryi*, in contrast to Gunnell and Yarborough who referred it to *E. minimus*, which is regarded here as a junior synonym of *E. gregoryi*. Gunnell and Yarborough, however, consider *E. gregoryi* a junior synonym of *E. borealis*.

The validity of *Eotitanops gregoryi* is supported by its small size and the presence of a p4 entoconid in the type, which distinguishes it from specimens of *E. borealis*, but makes it similar to specimens referred to *E. minimus*. Furthermore, Gunnell and Yarborough distinguished *E. borealis* from the smaller species (my *E. gregoryi*) by its large, elongated hypoconulid, whereas in the smaller species the hypoconulid is proportionately smaller. Although the distal part of the brontothere tooth row is highly variable and the size of the hypoconulid is probably a poor diagnostic character, the hypoconulid in the type of *E. gregoryi* is rather small in size and, thus, is similar to specimens of *E. minimus*, but different from specimens referred to *E. borealis*.

As stated above, Osborn (1929) designated a relatively complete skull (AMNH 14887) as the "neotype" for the type species of *Eotitanops* (*E. borealis*), but because the original type is still preserved, Osborn's specimen is nothing more than a referred specimen. Osborn (1929) argued that the facial region of this "neotype" skull is longer than the cranial region while in all other brontotheres the face is shorter than the cranium. This proportional difference was Osborn's main justification for separating *Eotitanops* from middle Eocene brontotheres such as *Palaeosyops*. Wallace (1980), however, pointed out that Osborn's interpretation

of the facial and cranial proportions of the "neotype" skull is questionable because the specimen is very fragmentary and the position of key morphological landmarks is uncertain. Wallace noted that *Eotitanops* is dentally similar to *Palaeosyops* and argued that until a more complete skull of *Eotitanops* is known, cranial proportions cannot be used to separate it from *Palaeosyops*. Wallace, therefore, regarded *Eotitanops* as a junior synonym of *Palaeosyops*.

Despite Wallace's valid objections, Mader (1989) argued that there are enough morphological differences between *Eotitanops* and *Palaeosyops* to justify separation of the two at the generic level. Mader noted that the left zygomatic arch of Osborn's "neotype" skull of *E. borealis* is complete and shows that this structure was thin and probably relatively straight. The zygomatic arch of *Eotitanops* was thus probably quite similar to the zygomatic arch of *Mesatirhinus*. In *Palaeosyops*, however, the zygomatic arch is very robust and sharply curved. Mader further argued that although much of the skull is lacking, the portions of the zygomatic arches and palate that are preserved suggest that the skull was dolichocephalic (as stated by Osborn 1929) or mesaticephalic. In contrast, all skulls of *Palaeosyops* are strongly brachycephalic, and this is a synapomorphic character of that genus.

Although the anterior dentition of Osborn's skull is incomplete, Mader also noted some differences between it and *Palaeosyops*. The left P1 is lacking entirely on Osborn's skull and the place on the maxilla to which it had been attached has been covered by plaster. The root of the left upper canine and all of the left P2 are, however, preserved. There is a long space between the left canine and left P2, so that no matter where the left P1 was originally placed there must have been a considerable diastema present. Skulls of *Palaeosyops* have either an extremely short diastema or no diastema at all.

Mader (1989) was unsure whether facial proportions could be used to distinguish *Eotitanops* from other brontotheres, but later (1991, 1998) concluded that Osborn was probably correct in asserting that the facial region of the "neotype" skull of *E. borealis* is proportionally much longer than in other brontothere genera. Mihlbachler (2008, p.375), however, cited a skull, unfortunately not illustrated, that he referred to *Eotitanops* (UCMP 132049) with a short face as in other brontotheres.

Until about twenty five years ago, classic rock units yielding specimens of *Eotitanops* (such as the Lostcabin Member of the Wind River Formation and upper part of Huerfano "A") were regarded as being Wasatchian in age (e.g., Robinson 1966; Savage & Russell 1983). Indeed, the original Wood Committee report (Wood *et al.* 1941) cited the first appearance of *Eotitanops* as one of the characteristics of the then newly named Wasatchian Land Mammal Age. In recent decades, however, strata yielding the earliest occurrence of *Eotitanops* have been regarded as being early Bridgerian (Gardnerbuttean) in age (Stucky 1984; Gunnell & Yarborough 2000; Zonneveld *et al.* 2000; and Robinson *et al.* 2004).

Species *Eotitanops borealis* (Cope 1880)

= *E. brownianus* (Cope 1881)
= *E. princeps* Osborn 1913
= *E. major* Osborn 1913?

Holotype: AMNH 4892, a right maxilla with complete P4 to M1 and fragmentary M2 to M3.

Referred specimens: AMNH 296 (type of *E. princeps*), AMNH 4885 (type of *E. brownianus*), AMNH 14887 (Osborn's "neotype" of *E. borealis*), AMNH 14888, AMNH 14890, and AMNH 14891.

Diagnosis: Large species of *Eotitanops* distinguished from *E. gregoryi* by its much larger size and lack of an entoconid on p4.

Discussion: Although many specimens were referred to *Eotitanops borealis* by Wallace (1980), the list of referred specimens in the present paper is limited to the type, Osborn's "neotype" skull of *E. borealis*, and the specimens that were used in the statistical analysis discussed above.

Species *Eotitanops gregoryi* Osborn 1913

= *E. minimus* Osborn 1919

Holotype: AMNH 14889, an incomplete lower jaw with some of the right cheek dentition intact and fragments of the left maxilla containing M2 and M3.

    Referred specimens: AMNH 17418, AMNH 17439 (type of *E. minimus*), AMNH 56539, AMNH 96281, AMNH 104773, YPM 16439, YPM 16462, UCM 24690, UCM 32171, UCM 42725, UCM 42740.

    Diagnosis: Small species of *Eotitanops* distinguished from *E. borealis* by its much smaller size and by the presence of an entoconid on p4.

    Discussion: This species is still poorly known and it is not absolutely certain that it belongs to the genus *Eotitanops*. The list of referred specimens for *Eotitanops gregoryi* cited above is taken from Wallace's unpublished Master's Thesis (1980) and consists of the specimens that he referred to *E. minimus*. According to Wallace, these specimens are from Huerfano Basin localities I, II, and V (see Robinson 1966), which are all in the upper Huerfano faunal zone (Gardnerbutte Local Fauna).

    According to Wallace, and confirmed here, a distinct entoconid is present on the p4 of all three specimens in the hypodigm (AMNH 17418, AMNH 17439, and AMNH 96281) that have this tooth preserved, although it is worn down on AMNH 96281.

    The entoconid on the p4 of the type of *Eotitanops gregoryi* (AMNH 14889) is smaller than the p4 entoconids of the two Huerfano specimens in which this tooth is well preserved. According to Wallace (1980, p. 28) the p4 entoconid in the type of *E. gregoryi* is not actually a cusp, but is simply a "crenellation" or "minor inflation" of the hypolophid, giving "the impression of incipient entoconid ... development". Although the entoconid is very small in the type of *E. gregoryi*, however, it is certainly a distinct cusp and not simply a "minor inflation". The Huerfano *E. gregoryi* sample is too small to determine the size variation of the p4 entoconid and it is possible that specimens will be discovered in which the p4 entoconid more closely approaches the size of this cusp in the type of *E. gregoryi*.

    Regardless of the character polarity of the p4 entoconid, the presence of this cusp in both the type of *Eotitanops gregoryi* and specimens once referred to *E. minimus*, in contrast with its absence in *E. borealis,* suggests a close relationship. These factors coupled with the close similarity in size between the type of *E. gregoryi* and specimens once referred to *E. minimus*, and the fact that the size variation among all of these individuals is well within the range of a single extant mammalian species, justifies synonymizing *E. gregoryi* and *E. minimus*.

    As noted, Gunnell and Yarborough (2000) regarded *E. gregoryi* as a junior synonym of *E. borealis* and regarded *E. minimus* as the valid name for the species described here.

Subfamily PALAEOSYOPINAE Steinmann and Döderlein 1890

Included genera: *Palaeosyops* (= *Limnohyus*, *Limnohyops*, *Eometarhinus*).

    Diagnosis: Same as for member genus, *Palaeosyops* (see below). Sister taxon to all brontothere subfamilies except for the Eotitanopinae (see cladogram in Mader 1998, Fig. 36.5)

    Discussion: *Palaeosyops* is the sole member of the Palaeosyopinae (Steinmann & Döderlein 1890). Because the subfamily Palaeosyopinae consist of only a single genus, the diagnosis of the subfamily does not differ from that of its member genus.

    Although Palaeosyopinae is recognized here as the valid name for this subfamily, it should be noted that the invalid name Limnohyinae predates it by fifteen years. Marsh (1875) compared *Diplacodon* to the "Limnohyidae," a previously unpublished family-group name. Marsh did not specify which taxa were to be included under this name, although it is obvious that it must include *Lymnohyus* (a junior synonym of *Palaeosyops*). According to the Principle of Coordination (Article 36, International Code of Zoological Nomenclature, Ride *et al*. 1999) this simultaneously established the subfamily name Limnohyinae with Marsh

(1875) as the author. If the names Limnohyidae and Limnohyinae were to be valid, therefore, the subfamily name Limnohyinae would be a senior synonym of Palaeosyopinae.

Although Marsh did not explicitly specify a type genus for the Limnohyinae, the subfamily name cannot be invalidated on this basis since the type genus (*Limnohyus*) can be clearly inferred from the construction of the name (Article 11.7.1.1 International Code of Zoological Nomenclature). Furthermore, even though the genus *Limnohyus* is now recognized as a junior synonym of *Palaeosyops*, the family-group name Limnohyinae cannot be invalidated on this ground (Article 40.1).

However, according to Article 11.7.1.2, in order for a family group name to be valid, it must be clearly used by the original author to "denote a suprageneric taxon and not merely as a plural noun or adjective referring to the members of a genus...". The name Limnohyinae is invalid, therefore, because it is not clear from the context of Marsh's paper whether the term Limnohyidae was intended to apply to *Limnohyus* and some of the other brontothere genera then recognized (such as *Palaeosyops* and *Telmatherium*), or merely to the three species of *Limnohyus* described by Marsh and Cope up to that time.

Genus *PALAEOSYOPS* Leidy 1870

= *Limnohyus* Marsh 1872
= *Limnohyops* Marsh 1890
= *Eometarhinus* Osborn 1919

Age: Bridgerian.
    Subage: Gardnerbuttean, Blacksforkian, and Twinbuttean.
    Type species: *P. paludosus* Leidy 1870.
    Included species: *P. fontinalis* (Cope 1873a); *P. robustus* (Marsh 1872).
    Diagnosis: Medium-sized (length P2 to M3 approximately 123 to 165 mm) brontothere with six upper and lower incisors; large canines; very small or no upper diastema and a moderate lower diastema (mostly between p1 and p2); unmolarized premolars; large paraconules on the molars; hypocone or pseudohypocone variably present on M3. *Palaeosyops* is distinguished from all other brontotheres by the following synapomorphies: strongly brachycephalic skull; robust zygomatic arches that are sharply curved; sharply curved nasals that taper distally; and a low convexity or dome in the region of the frontoparietal border (see Figure 6).

    Discussion: Leidy based the type species of *Palaeosyops*, *P. paludosus*, on four isolated teeth collected from Church Buttes in the Green River Basin of Wyoming (Leidy 1870). Of these cotypes, Osborn (1929) selected USNM 759, a lower second molar, as the lectotype for the type species.

    Based on the length and width of the lectotype molar, Mader (1989) concluded that the type belongs to the same taxon as the medium-sized, brachycephalic brontotheres later named *Limnohyus* and *Limnohyops* by Marsh (see Figure 6). Because the lectotype appeared to be identifiable, Mader accepted the name *Palaeosyops* as valid, but noted that if the lectotype should prove to be inadequate for diagnostic purposes, the next available name would be *Limnohyus* Marsh (1872; type species *L. robustus*), which is based on a relatively complete skull (YPM 11122). The lectotype of *Palaeosyops paludosus* is from the Blacks Fork Member of the Bridger Formation, and because only one brontothere genus has been reliably recorded from this level, it is almost certain that *Palaeosyops* is a valid taxon.

    Within two years after Leidy's naming of *Palaeosyops paludosus*, Marsh recognized that some of the specimens that had been referred to *Palaeosyops* had a hypocone on the M3 and some did not. Marsh (1872) proposed that the name *Palaeosyops* be restricted to those animals with a hypocone and that the name *Limnohyus* be given to those without it. Leidy (1872b), however, pointed out that the absence of a hypocone was a character originally attributed to *Palaeosyops* (the type series of *Palaeosyops paludosus* included an M3 that lacked a hypocone) and could not be used to define a new genus. Marsh later (1890) reversed his previous position and applied the name *Palaeosyops* to specimens without the hypocone on M3 and gave the new generic name *Limnohyops* to those with one.
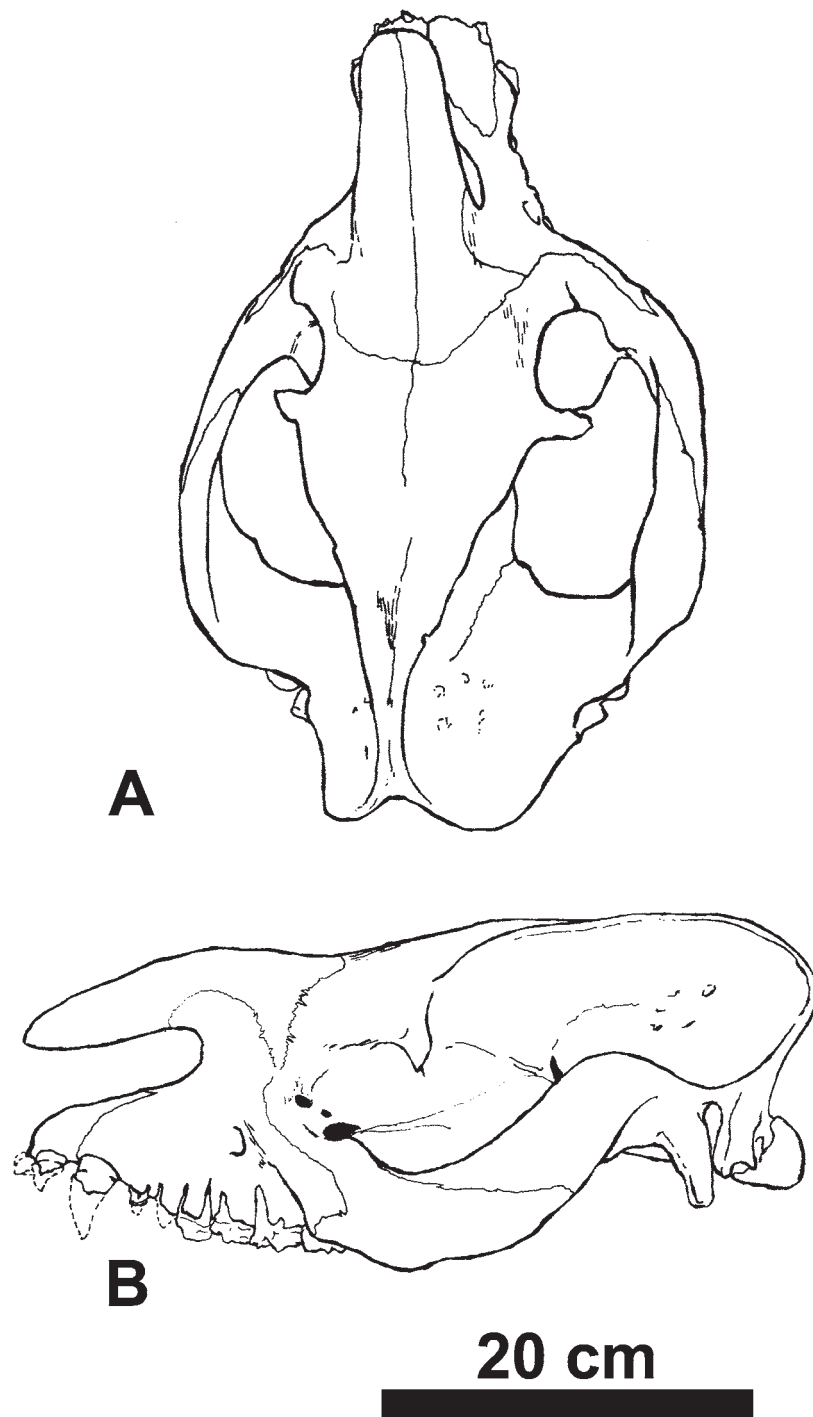
FIGURE 6. Skull of *Palaeosyops* in **A**, dorsal, and **B**, lateral views. After Osborn (1929).

Earle (1891; 1892) recognized both *Limnohyops* and *Palaeosyops* as valid genera as did Osborn (1908; 1929). Osborn (1929) diagnosed the genus *Limnohyops* as follows:

Brachycephalic; grinding teeth persistently brachydont; conules on the molars persistent, usually lophoid; third superior molar subquadrate and usually with distinct hypocone. Proportions of skull and skeleton moderately robust. Manus slender. Five sacral vertebrae (type).

Osborn's (1929) formal diagnosis for the genus *Palaeosyops*, which he incorrectly characterized as specific rather than generic characters (p. 312), was very similar to the above:

Brachycephalic. Grinding teeth persistently brachydont; metaconules on the molars persistent or absent; third superior molar without hypocone. Skull and skeleton robust; feet broad; manus with well-developed fifth digit; lunar resting subequally on magnum and unciform. Four sacral vertebrae.

Osborn (1929, p. 302) stated that the ancestral members of these two genera from Bridger B (Blacks Fork Member of the Bridger Formation) are difficult to distinguish from one another and elsewhere (p. 303) commented that the early species of both genera are so similar that they might be included within a single genus. According to Osborn, however, distinctions gradually began to develop between the two genera until, in the upper strata of the Bridger Formation, the two forms are quite distinct. Osborn listed ten characters (pp. 302–303) that supposedly distinguish species of *Limnohyops* and *Palaeosyops* from higher geologic levels (such as *P. robustus* and *L. laticeps* from Bridger D). These characters (not quoted verbatim) are:

1. Upper and lower molars of *Palaeosyops* relatively larger, more rounded, and more robust.

2. Vertical striations on the cones of the upper and especially lower molars more distinct in *Palaeosyops*.

3. Conules on M1–2 of *Palaeosyops* more variable, more rounded, and separate; in *Limnohyops* more constant, lophoid, ridged, or conjoined with the protocone and hypocone. Osborn noted that this distinction is not always reliable.

4. In *Limnohyops* hypocone of M3 typically present; in *Palaeosyops*, typically absent. In *Limnohyops* metaconule of M3 extremely reduced (owing to the large size of the adjacent hypocone); in *Palaeosyops* metaconule usually present and sometimes in such close proximity to the raised posterior cingulum that it appears similar to a hypocone (Osborn called such a structure a "pseudohypocone"). Thus the M3 of *Limnohyops* is more quadrate and that of *Palaeosyops* is generally more triangular.

5. In *Palaeosyops* parastyle rounded and obliquely placed across the outer angle of the crown; in *Limnohyops* parastyle sharp and extending outward as a ridge.

6. In *Palaeosyops* nasals taper toward the extremities and are more pointed, while in *Limnohyops* the sides of the nasals are more parallel and they are more truncate at the extremities.

7. In *Palaeosyops* the suborbital bar is rounded and the maxillary process extends across its lower side as a broad splint. In *Limnohyops* the bar is more depressed and slightly rectangular in section and the maxillary process extends across its lower side as a thin splint.

8. In *Palaeosyops* there is a strong median convexity near the frontoparietal junction, while in *Limnohyops* the top of the cranium is slightly concave.

9. The sagittal crest of *Palaeosyops* is lower, broader, and passes more rapidly into the temporal ridges whereas in *Limnohyops* the crest is higher and thinner and extends well forward before spreading into the temporal ridges.

10. Male jaws of *Palaeosyops* have a more prominent, massive chin and shorter insertion for the digastric than male skulls of *Limnohyops*. The rami of *Palaeosyops* (seen from below) are more massive than those of *Limnohyops* and the anterior border of the coronoid process in *Palaeosyops* is broader. In more progressive stages of *Palaeosyops* the anterior border of the coronoid process is hollowed out in front while in progressive stages of *Limnohyops* the process is narrower, less deeply excavated, and "lies more to the outer side of the line of the molar teeth".

Despite Osborn's recognition of *Palaeosyops* and *Limnohyops* as distinct genera, he noted (1929, p. 303) that the divergence between *Palaeosyops* and *Limnohyops* is far less than that observed within the modern genus *Cervus*. Mader (1989) concluded that *Palaeosyops* and *Limnohyops* are synonymous and stated that most of the generic distinctions cited by Osborn may be attributed to the vagaries of preservation or to individual variation. Gunnell and Yarborough (2000) also regarded *Palaeosyops* and *Limnohyops* as synonyms.

The following can be attributed to individual variation and probably sexual dimorphism in the above characters: the size and massiveness of the molars, the distinctiveness of the striations on the molars, the shape of the sagittal and temporal crests (see Mader 1989), and the shape and massiveness of the lower jaw (characters 1, 2, 9, and 10). The shape of the parastyle (character 5) is also probably attributable to individual

variation and possibly sexual dimorphism, but may also reflect differences in wear. The presence or absence of a hypocone on M3 (character 4) is attributable to individual variation, but is not a sexually dimorphic character.

Osborn was incorrect in his assertion that skulls of "*Limnohyops*" lack the frontoparietal convexity or dome (character 8). Although he illustrated a skull (Osborn 1929; Figs. 256, 259) that clearly shows a concave rather than convex forehead, the specimen in question (AMNH 11687) is almost crushed flat and this cranial morphology cannot be inferred. As previously noted (Mader 1989), the frontoparietal area is not well preserved in any of the specimens that Osborn referred to *Limnohyops*, with most being badly damaged or missing entirely. The dome appears to be present in all specimens of *Palaeosyops*, but is more prominent in the supposed males.

The most convincing character used by Osborn to distinguish *Limnohyops* from *Palaeosyops* is the shape of the suborbital bar and the configuration of the suture pattern between the jugal and maxilla (character 7). Figure 7 illustrates two specimens showing these suture patterns: AMNH 5104, which Osborn referred to *Limnohyops* (type of *L. laevidens*); and AMNH 1516, which Osborn referred to *Palaeosyops*. In AMNH 1516 a wide flange of the maxilla extends below the jugal and forms the ventral surface of the zygomatic arch beneath the orbit. In AMNH 5104 only a slender projection of the maxilla extends onto the zygomatic arch, and the suture between the jugal and maxilla has a distinct Z-shaped pattern. Furthermore, the suborbital part of the zygomatic arch is broadly rounded in AMNH 1516 and is somewhat angular in AMNH 5104. Although seemingly excellent distinguishing characteristics, these most likely reflect preservational rather than taxonomic differences. In both specimens the morphology of the jugal beneath the orbit is the same and the uppermost contact between the jugal and maxilla in AMNH 5104 is in the same position as the long oblique contact between the jugal and maxilla in AMNH 1516.

I posit that the morphology of both specimens was originally the same but, in AMNH 5104 the ventral part of the wide flange of the maxilla beneath the jugal has been broken away revealing the bottom part of the Z-shaped pattern normally concealed beneath. The ventral part of the maxillary flange is responsible for the roundness of the suborbital bar cited by Osborn as a character for *Palaeosyops*. When this flange is broken away, however, it results in the angular morphology that Osborn attributed to *Limnohyops*. Figure 8 illustrates AMNH 5104 showing my suggested reconstruction of the jugal-maxilla contact in this specimen. At least one other specimen that Osborn referred to *Limnohyops* (AMNH 11687, type of *L. priscus*) appears to have the jugal-maxillary region broken in a manner similar to that of AMNH 5104.

Osborn recognized five valid species of *Limnohyops* and eight of *Palaeosyops*. These species were generally delineated by size, morphology of the premolars (shape of P2, presence of a mesostyle on some of the premolars, and presence of two lingual cusps on P2), and by the shape of the skull. The differences in premolar morphology cited by Osborn are trivial, however, and many of the differences in cranial morphology are the result of taphonomic deformation.

In 1919 Osborn described a fragmentary skull (AMNH 17412, Figure 9) from the Huerfano Basin and identified it as a form ancestral to *Metarhinus*, which he named *Eometarhinus* ("Dawn *Metarhinus*"). In 1929 Osborn upheld this identification, but Robinson (1966), Wallace (1980), Mader (1989; 1998), and Gunnell and Yarborough (2000) synonymized *Eometarhinus* with *Palaeosyops*.

Because all of the Huerfano material referred to *Palaeosyops* is rather poorly preserved it is difficult to demonstrate with certainty that it represents the same genus as *Palaeosyops* from the Bridger Formation. Although the Huerfano material is here considered to be correctly referred to *Palaeosyops,* I have previously questioned whether they are truly the same (Mader 1989). The upper part of the Huerfano Formation, therefore, preserves the earliest known record of *Palaeosyops* in North America. Unfortunately, only a few specimens have been collected from this stratigraphic level and I have data for only two individuals: AMNH 17411 and AMNH 17425.

The Blacks Fork Member of the Bridger Formation is stratigraphically higher than the Huerfano Formation and is divisible into two stratigraphic levels: Bridger A and Bridger B. The sample of *Palaeosyops* from Bridger A that was examined for the present study includes some well-preserved cranial material, but is rather small in size and I have collected data for only three individuals from this level: AMNH 5107 (the type

of *P. fontinalis*), UW 3039, and UW 3091. Most of the *Palaeosyops* material known from the Blacks Fork Member of the Bridger Formation is from Bridger B. I have data for twenty five individuals from this higher level.

The Twin Buttes Member of the Bridger Formation overlies the Blacks Fork Member and is similarly divisible into two stratigraphic levels: Bridger C and Bridger D. Altogether data for 16 individuals from the Twin Buttes Member were collected for this study: 9 from Bridger C, 4 from Bridger D, and 3 from uncertain stratigraphic levels within the unit.
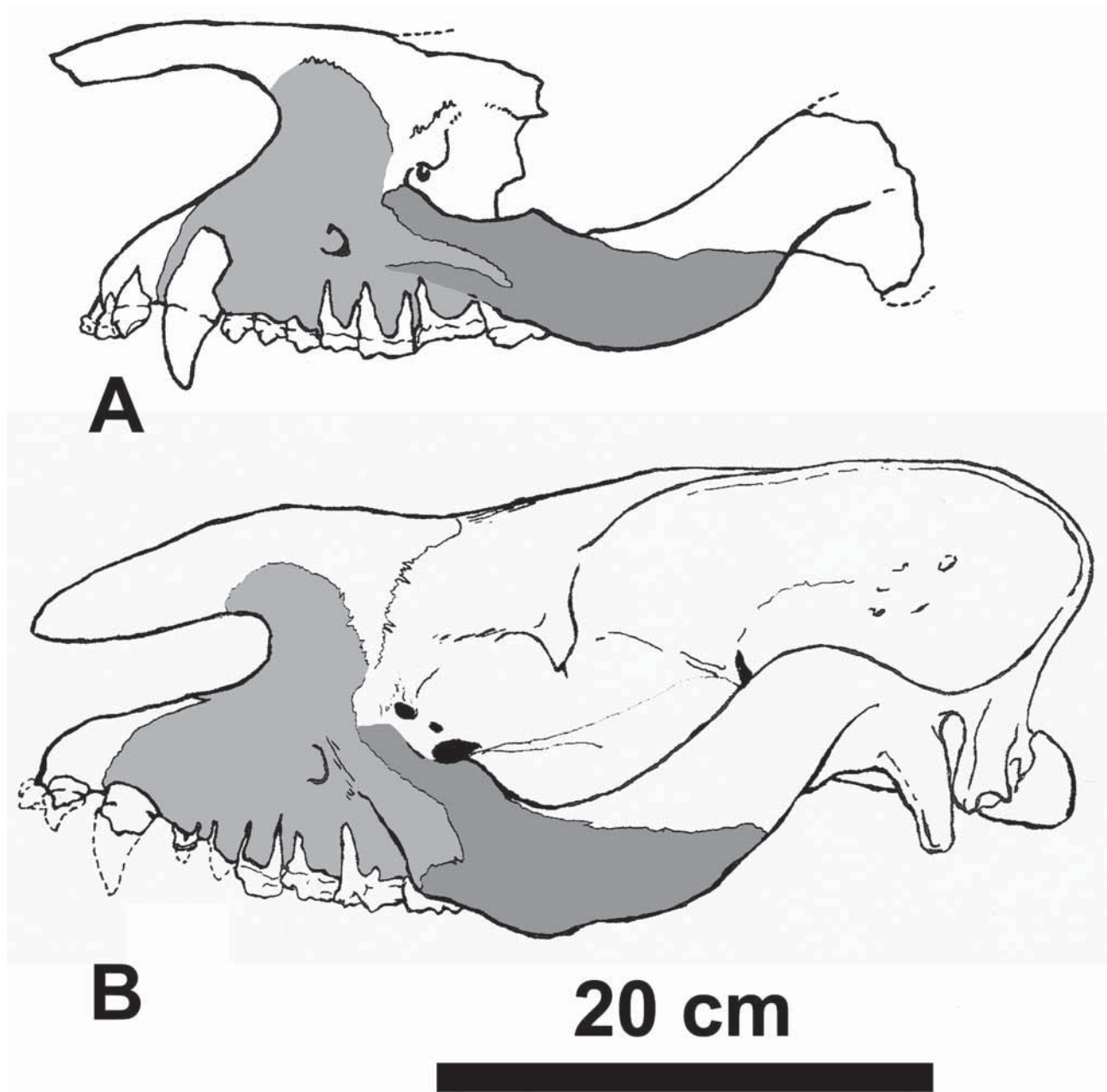

FIGURE 7. Suture pattern between the jugal (dark gray) and maxilla (light gray) in two specimens of *Palaeosyops*. **A**, AMNH 5104 (reversed), referred by Osborn to *Limnohyops*; **B**, AMNH 1516 (reversed), referred by Osborn to *Palaeosyops*. Both figures modified from Osborn (1929).
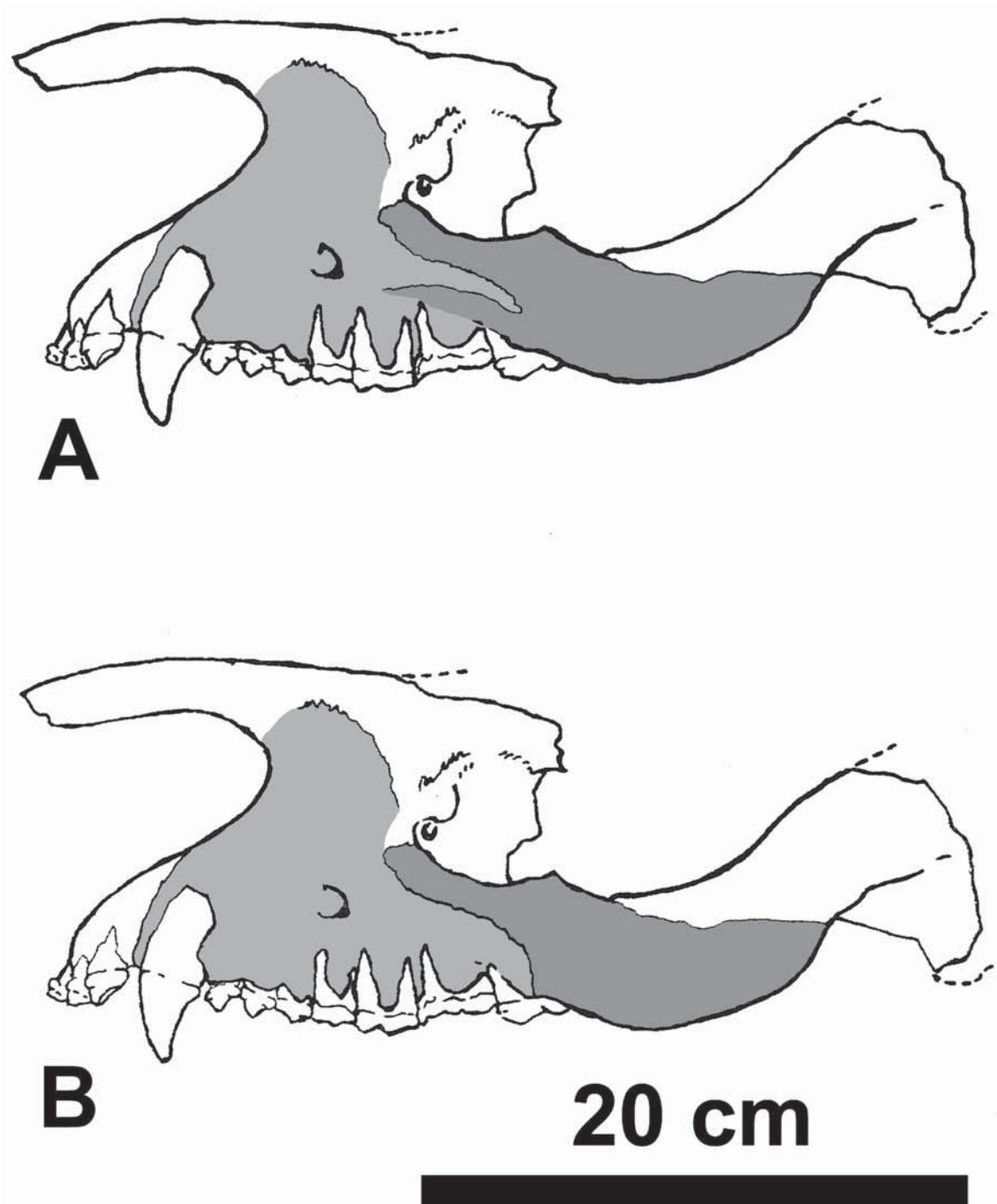
FIGURE 8. Suture pattern between the jugal (dark gray) and maxilla (light gray) in AMNH 5104, a specimen of *Palaeosyops paludosus*. **A**, suture pattern as it actually appears on the specimen, probably due to breakage of the maxilla; **B**, reconstruction of the jugal-maxilla contact as it may have originally appeared. Both figures reversed and modified from Osborn (1929).

The sample sizes of *Palaeosyops* from the Huerfano Formation (assuming the generic assignment is correct) and Bridger A assembled for the present study are too small to make a statistical analysis meaningful. Thus it is not practical to compare specimens from the Huerfano Formation against those from Bridger A using *t*-tests, nor is it profitable to examine summary statistics for specimens of *Palaeosyops* from each level. The most complete specimen of *Palaeosyops* from Bridger A examined for this study (UW 3091, Figure 10) appears to be rather different compared to specimens from Bridger B and may be taxonomically distinct. Compared to specimens of *Palaeosyops* from Bridger B, the lingual cusp on the second upper premolar of

UW 3091 is very poorly developed and the metacone is almost lacking (although not all specimens of *Palaeosyops* from Bridger A have a P2 that is as structurally plesiomorphic). Furthermore, the distinct cranial convexity that I have regarded (Mader 1989; 1998; present paper) as a synapomorphy of *Palaeosyops* appears to be very small and may be absent entirely (it is difficult to be certain because of crushing). There is some evidence of a slight swelling in the fronto-parietal region, however (see Figure 10). Gunnell and Yarborough (2000) have also described a specimen of *Palaeosyops* from the lower Bridger (UM 94880) with a very small dome. The small dome (compared to specimens of *Palaeosyops* from higher levels) could be a species characteristic, but it is also possible that it is a characteristic of females (Mader 1989).
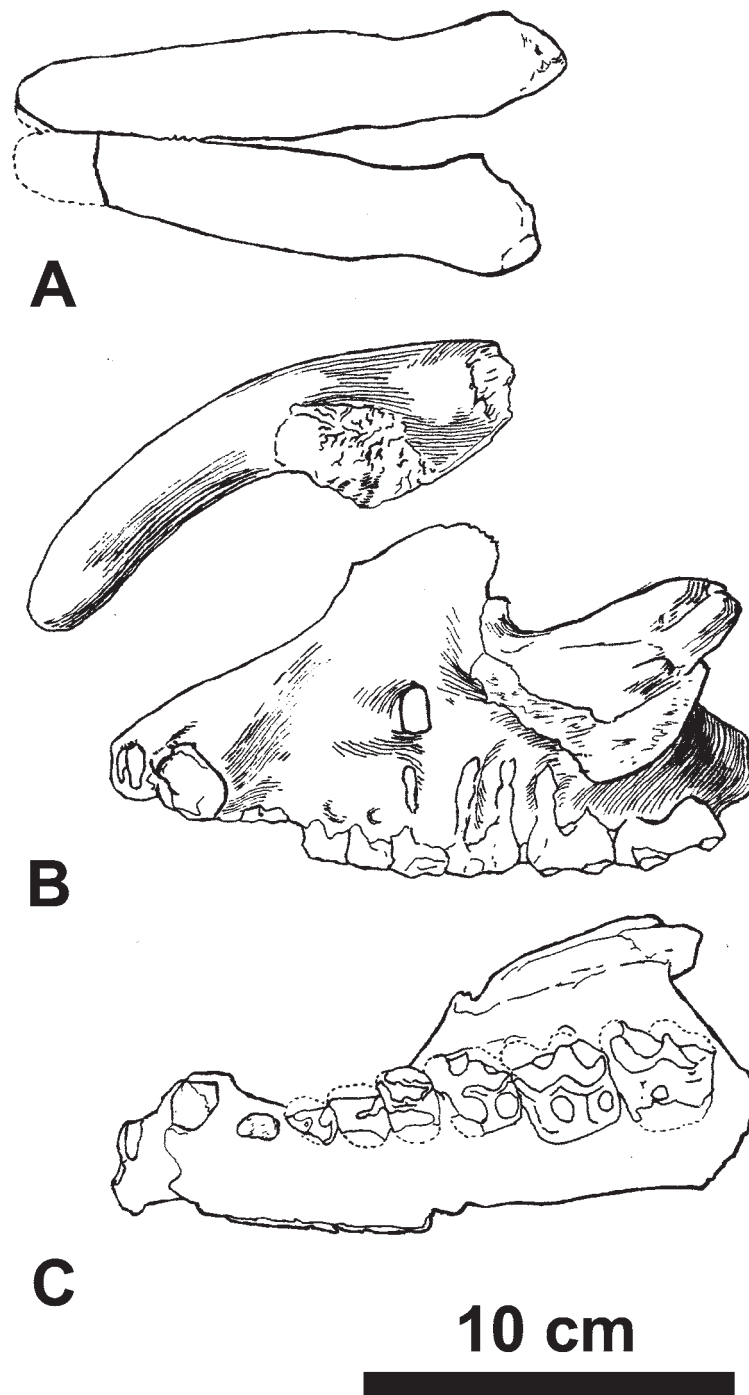

FIGURE 9. Holotype (AMNH 17412) of "*Eometarhinus*" *huerfanensis* (= *Palaeosyops fontinalis*). **A**, nasals in dorsal view; **B**, nasals and facial region of skull in lateral view; and **C**, palate in ventral view. After Osborn (1929).

FIGURE 10. Skull of *Palaeosyops fontinalis* (UW 3091) in lateral view.

Other cranial and dental characters of UW 3091 closely match those of specimens from Bridger B including a strongly brachycephalic skull and robust, sharply downturned zygomatic arches. The nasals are missing from the specimen, however, and it is not known whether they are strongly arched and distally tapered as in specimens of *Palaeosyops* from Bridger B. Gunnell and Yarborough (2000) noted that the nasals of UM 94880 are curved ventrally, but do not appear to taper distally. If correct, then distally tapered nasals could not be a synapomorphic character of *Palaeosyops* (as formulated here), but would be a shared derived character of the more derived *Palaeosyops* species (*P. paludosus* and *P. robustus*). Gunnell and Yarborough's specimen is crushed, however, (which could flatten and, thus, widen the tips of the nasals) and the type of "*Eometarhinus*" *huerfanensis* (here referred to *Palaeosyops*) has nasals that taper distally (see Figure 9).

Because of the small size of specimens of *Palaeosyops* from Bridger A and the retention of plesiomorphic conditions in at least one specimen of *Palaeosyops* from this level (UW 3091), I provisionally accept the specimens from Bridger A as representing a species that is distinct from specimens from Bridger B. The type of *P. fontinalis* is from Bridger A, and I tentatively refer all of the *Palaeosyops* material from this level to that species. I also tentatively refer specimens of *Palaeosyops* from the Huerfano Formation to *P. fontinalis* because of their relatively small size and because there is no basis at present for distinguishing them from specimens of *Palaeosyops* from Bridger A. Many more fairly complete specimens of *Palaeosyops* from Bridger A and from the Huerfano Formation will have to be collected and analyzed before either of these conclusions can be accepted with reasonable certainty. If it should later prove that the material from the Huerfano Formation represents a distinct species, then the name *P. huerfanensis* (Osborn) could probably be applied to it.

Table 7 presents the summary statistics for the sample of *Palaeosyops* from Bridger B. Almost 90 % of the individual coefficients of variation fall within the ideal range of 4 to 10. Three variables (excluding diastema length) have values of V greater than 10 (rounded to the nearest whole number) and one has a value of V less than 4. Although the average coefficient of variation for the sample is slightly high (6.7) it is within the range that I accept for a single species. Two out of the three variables that have values of V greater than 10 are measurements of canine size. Canine size is often sexually dimorphic in perissodactyls and it is possible that this factor accounts for the high individual values of V and perhaps for the relatively high average value of V. Although I have previously stated that canine size is not sexually dimorphic in brontotheres (Mader 1989) I have since concluded that canine size is sexually dimorphic in at least some, and possibly all, brontotheres (Mader 1998). Gunnell and Yarborough offer evidence suggesting that canine size may be dimorphic in

Palaeosyops (see Gunnell & Yarborough 2000, Fig. 12). If canine size is excluded from the calculation of the average value of V for the sample, then the average value becomes 6.4, which is within the ideal range suggested by Simpson *et al*. (1960).

TABLE 7. Summary statistics for specimens of *Palaeosyops* from Bridger B (all measurements in millimeters).

	n	Range	M	s	V
Basilar Length Skull[a]	4	396.8 – 421.5	409.2	±10.5	2.6
Length Cheek Tooth Series[a]	8	142.0 – 167.0	155.2	±8.4	5.4
Length P2 to M3[a]	12	129.0 – 161.0	144.0	±8.7	6.0
Length Premolar Series[a]	11	51.0 – 68.0	63.2	±5.1	8.1
Length Molar Series[a]	17	84.5 – 105.8	92.4	±5.9	6.3
Length Diastema[a]	9	4.6 – 11.0	6.7	±2.1	31.2
Length Left M3	17	30.5 – 38.0	34.0	±2.0	6.0
Length Right M3	19	30.0 – 39.5	33.4	±2.5	7.4
Width Left M3	15	32.8 – 39.4	35.9	±2.3	6.3
Width Right M3	17	30.5 – 41.3	35.7	±2.7	7.5
Length Left M2	15	31.0 – 36.5	33.5	±1.8	5.5
Length Right M2	16	29.0 – 36.5	32.7	±2.2	6.6
Width Left M2	15	30.7 – 38.3	34.7	±2.2	6.3
Width Right M2	13	30.0 – 39.4	34.9	±2.8	7.9
Length Left M1	12	25.0 – 29.0	27.2	±1.4	5.2
Length Right M1	16	23.5 – 29.0	26.2	±1.9	7.3
Width Left M1	13	25.3 – 29.9	27.6	±1.6	5.8
Width Right M1	12	25.3 – 30.0	27.2	±1.5	5.4
Length Left P4	14	17.0 – 19.5	18.4	±0.8	4.3
Length Right P4	14	16.0 – 20.5	17.7	±1.2	6.6
Width Left P4	15	20.7 – 26.0	23.8	±1.5	6.3
Width Right P4	14	22.5 – 26.4	24.1	±1.3	5.5
Length Left P3	12	15.0 – 17.5	16.3	±0.7	4.4
Length Right P3	15	13.0 – 17.0	15.8	±1.0	6.4
Width Left P3	10	17.4 – 20.9	19.5	±1.1	5.6
Width Right P3	11	17.9 – 21.3	19.6	±1.3	6.5
Length Left P2	11	12.0 – 16.5	13.8	±1.2	8.3
Length Right P2	13	11.0 – 17.0	14.0	±1.6	11.3
Width Left P2	9	13.0 – 16.4	14.8	±1.0	6.7
Width Right P2	8	13.2 – 16.0	14.6	±1.0	6.6
Buccal-Lingual Width Left Canine	5	17.5 – 22.9	20.5	±2.3	11.4
Buccal-Lingual Width Right Canine	2	19.4 – 22.5	20.9	±2.2	10.6
Mesial-Distal Width Left Canine	5	19.4 – 24.4	22.1	±2.1	9.4
Mesial-Distal Width Right Canine	2	21.0 – 23.1	22.0	±1.5	6.6
AVERAGE V					6.7[b]

[a] Based, whenever possible, on an average of left and right measurements. [b] Excluding Diastema Length.

Analysis of the coefficient of variation strongly suggests that the sample is homogeneous and represents only a single species. It is surprising, therefore, that cluster analysis has revealed the presence of two or more size groups among the specimens in the sample. A cluster analysis of all of the variables listed in Table 7 results in a dendrogram (Figure 11) in which all of the specimens are distributed in an essentially homogeneous manner. If, however, cluster analyses are performed on certain groups of variables, then size groups of specimens begin to emerge.

FIGURE 11. Cluster dendrogram for specimens of *Palaeosyops* from Bridger B resulting from a cluster analysis of all variables listed in Table 7. **a**, type of *Limnohyops monoconus*; **b**, type of *Limnohyops priscus*; **c**, type of *Limnohyus laevidens*.

If, for example, a cluster analysis is performed using only the length of the cheek tooth series, length of the cheek tooth series exclusive of P1, length of the molar series, and the basilar length of the skull, then a dendrogram results in which three groups are delineated (Figure 12). Two of these groups (labeled Group 1

and Group 2 on the diagram) join at a distance of 2.5 millimeters and are then joined by a third group (Group 3) at 4.0 millimeters. One specimen (AMNH 5102) groups out separately joining the others at a distance of 7.25 millimeters.
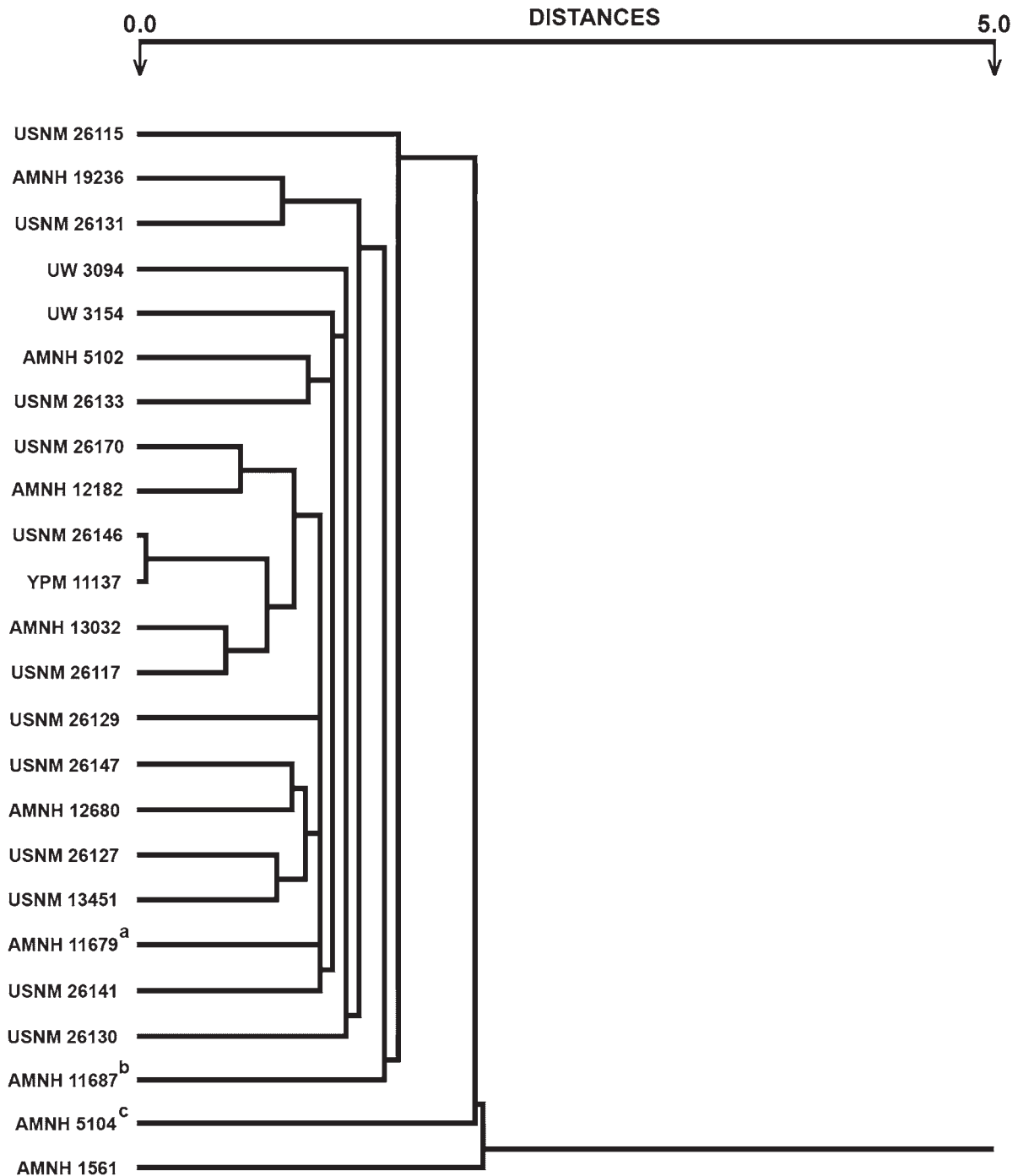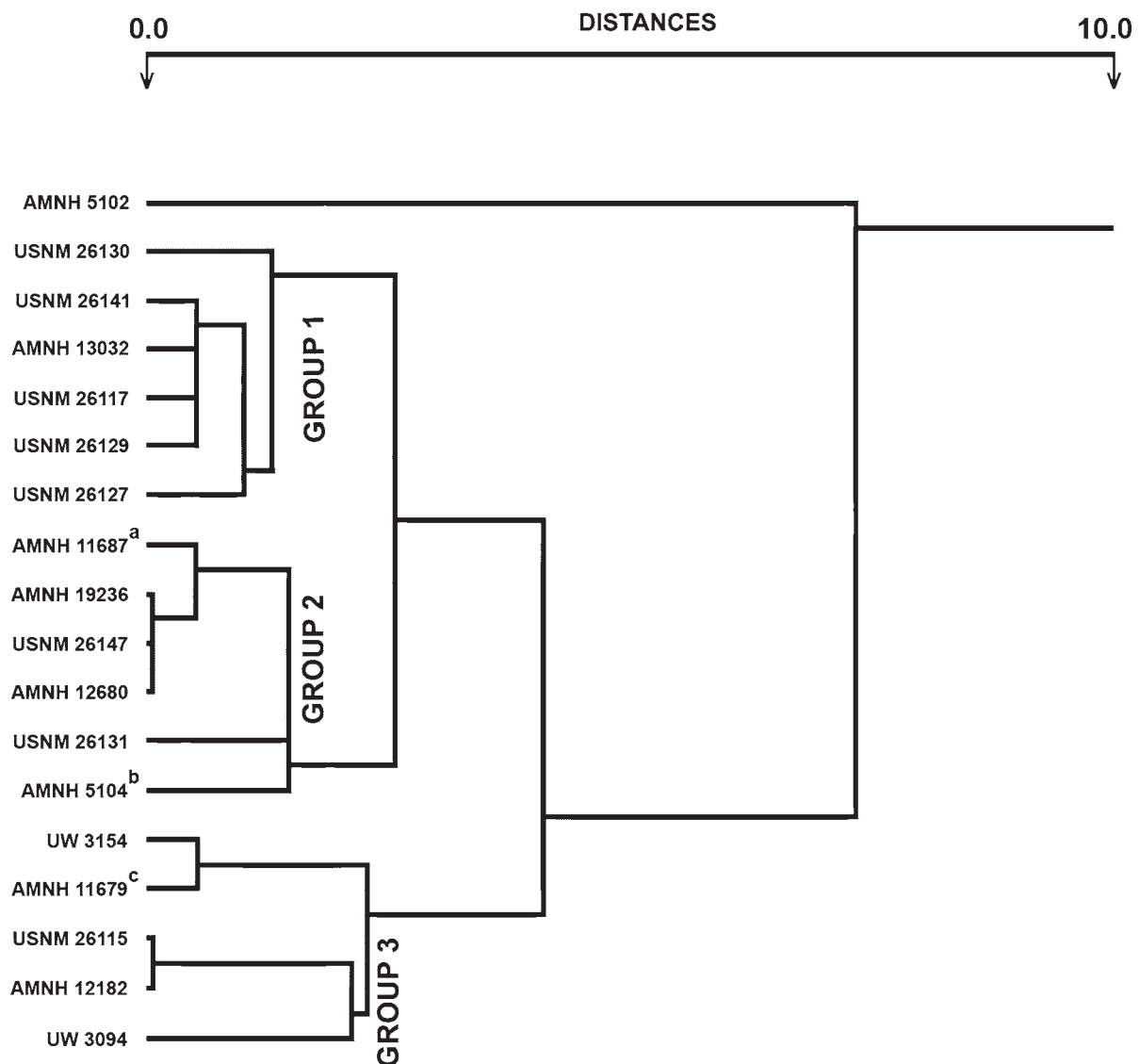

FIGURE 12. Cluster dendrogram for specimens of *Palaeosyops* from Bridger B resulting from a cluster analysis of basilar skull length, length of cheek tooth series, length of cheek tooth series exclusive of P1, and length of molar series. **a**, type of *Limnohyops priscus*; **b**, type of *Limnohyus laevidens*; **c**, type of *Limnohyops monoconus*.

If a third cluster analysis is performed using only the length and width of the first upper molar, then only two distinct size groups emerge (Figure 13). The size difference between these two groups is extremely small, however, and both join on the dendrogram at a distance of only one millimeter. It is difficult to determine from these cluster analyses how many size groups are actually present in the sample. Because the cluster analysis of the first upper molar resulted in the sharpest delineation of size groups, the groups suggested by this analysis were analyzed further.

T-tests (Tables 8 and 9) confirm that for many variables (length of cheek tooth series, length of cheek tooth series exclusive of P1, length of molar series, width of M3, length and width of M2 and M1, and width right P4) the means of the two size groups suggested by the dendrogram in Figure 13 are significantly different. Because the length of the premolar series and all but one of the individual premolar measurements show no significant difference between the two size groups, it is probable that molar dimensions account for the significant difference observed for the length of the cheek tooth series (with or without P1).

TABLE 8. F-Test comparisons for the large-size group (Group 1) and small-size group (Group 2) of *Palaeosyops* from Bridger B.

	n Group 1	n Group 2	F	Probability	*T*-Test
Basilar Length Skull[a]	3	1	———	———	———[b]
Length Cheek Tooth Series[a]	4	3	0.165	0.686	Pooled
Length P2 to M3[a]	7	4	0.128	0.721	Pooled
Length Premolar Series[a]	4	5	3.935	0.049	Separate
Length Molar Series[a]	7	8	0.472	0.492	Pooled
Length Diastema[a]	4	3	0.238	0.628	Pooled
Length Left M3	9	6	0.006	0.936	Pooled
Length Right M3	7	8	3.806	0.052	Separate
Width Left M3	8	6	1.555	0.213	Pooled
Width Right M3	7	6	0.895	0.345	Pooled
Length Left M2	8	5	0.255	0.614	Pooled
Length Right M2	7	7	2.212	0.138	Pooled
Width Left M2	8	6	0.260	0.610	Pooled
Width Right M2	6	5	0.317	0.574	Pooled
Length Left M1	8	4	0.155	0.694	Pooled
Length Right M1	8	8	0.549	0.459	Pooled
Width Left M1	9	4	2.528	0.113	Pooled
Width Right M1	5	7	0.853	0.357	Pooled
Length Left P4	8	5	0.578	0.448	Pooled
Length Right P4	6	6	0.244	0.621	Pooled
Width Left P4	8	5	0.037	0.849	Pooled
Width Right P4	7	6	2.698	0.101	Pooled
Length Left P3	7	3	1.960	0.165	Pooled
Length Right P3	7	6	4.086	0.044	Separate
Width Left P3	6	3	0.684	0.410	Pooled
Width Right P3	5	4	0.002	0.964	Pooled
Length Left P2	6	3	6.123	0.015	Separate
Length Right P2	8	3	2.660	0.106	Pooled
Width Left P2	5	2	0.003	0.956	Pooled
Width Right P2	6	2	0.003	0.958	Pooled
Buccal-Lingual Width Left Canine	2	2	0.305	0.591	Pooled
Buccal-Lingual Width Right Canine	1	0	———	———	———[b]
Mesial-Distal Width Left Canine	2	2	0.139	0.716	Pooled
Mesial-Distal Width Right Canine	1	0	———	———	———[b]

[a] Based, whenever possible, on an average of left and right measurements. [b] There is no variance in at least one of the two groups being compared.

Taking all *t*-tests together, there is an 80% chance (see Methods section) that at least one of these significant results is invalid (i.e., a false rejection of the null hypothesis). If, however, the error analysis is restricted to only those measurements that involve the molars (length of cheek tooth series, length of cheek tooth series exclusive of P1, length of molar series, and length and width of individual molars) then there is only a 54% chance that at least one of the significant results is due to a Type I error.

TABLE 9. *T*-Test comparisons for the two size groups of *Palaeosyops* from Bridger B

	T	DF	Probability
Basilar Length Skull[a]	——[b]	——	——
Length Cheek Tooth Series[a]	3.164	5.0	0.025
Length P2 to M3[a]	2.363	9.0	0.042
Length Premolar Series[a]	1.018[c]	4.7	0.366
Length Molar Series[a]	3.069	13.0	0.009
Length Diastema[a]	0.649	5.0	0.545
Length Left M3	1.516	13.0	0.153
Length Right M3	1.634[c]	8.0	0.141
Width Left M3	2.215	12.0	0.047
Width Right M3	3.129	11.0	0.010
Length Left M2	2.180	11.0	0.052
Length Right M2	4.900	12.0	0.000
Width Left M2	5.802	12.0	0.000
Width Right M2	4.143	9.0	0.003
Length Left M1	6.125	10.0	0.000
Length Right M1	9.335	14.0	0.000
Width Left M1	6.169	11.0	0.000
Width Right M1	4.130	10.0	0.002
Length Left P4	1.863	11.0	0.089
Length Right P4	1.658	10.0	0.128
Width Left P4	1.488	11.0	0.165
Width Right P4	2.286	11.0	0.043
Length Left P3	0.086	8.0	0.933
Length Right P3	1.808[c]	6.3	0.121
Width Left P3	1.468	7.0	0.186
Width Right P3	1.818	7.0	0.112
Length Left P2	0.379[c]	2.1	0.741
Length Right P2	0.156	9.0	0.880
Width Left P2	0.802	5.0	0.459
Width Right P2	1.548	6.0	0.173
Buccal-Lingual Width Left Canine	0.414	2.0	0.719
Buccal-Lingual Width Right Canine	——[b]	——	——
Mesial-Distal Width Left Canine	0.478	2.0	0.680
Mesial-Distal Width Right Canine	——[b]	——	——

[a] Based, whenever possible, on an average of left and right measurements. [b] Insufficient data for *t*-test. [c] Separate *t*-test

The summary statistics for the two size groups suggested by the dendrogram in Figure 13 are presented in Tables 10 and 11. In Table 10, 75 % of the individual values of V (rounded to the nearest whole number) for the larger-size group are within the range expected for a single species. The average value of V for the sample (exclusive of diastema length and variables where n=1) is also within the recognized parameters of a single species (= 4.9) although, as indicated above, canine size might be sexually dimorphic and thus influence this result. If canine size is excluded from the calculation of the average, however, the average value of V remains within the suggested parameters of a single species (= 4.6).

TABLE 10. Summary statistics for the large-size group of *Palaeosyops* from Bridger B (all measurements in millimeters).

	n	Range	M	s	V
Basilar Length Skull[a]	3	396.8 – 421.5	410.3	±12.5	3.1
Length Cheek Tooth Series[a]	4	156.0 – 167.0	161.6	±4.9	3.0
Length P2 to M3[a]	7	141.0 – 161.0	148.8	±6.7	4.5
Length Premolar Series[a]	4	63.5 – 67.5	65.1	±1.7	2.7
Length Molar Series[a]	7	91.0 – 105.8	96.9	±5.3	5.5
Length Diastema[a]	4	4.7 – 11.0	7.7	±2.6	34.3
Length Left M3	9	32.5 – 38.0	34.2	±1.8	5.1
Length Right M3	7	31.0 – 39.5	34.4	±2.8	8.1
Width Left M3	8	32.9 – 39.2	36.6	±2.2	6.0
Width Right M3	7	34.4 – 39.4	37.1	±1.9	5.0
Length Left M2	8	31.5 – 36.5	34.0	±1.7	4.9
Length Right M2	7	33.0 -36.5	34.6	±1.5	4.5
Width Left M2	8	34.1 – 38.3	36.3	±1.3	3.6
Width Right M2	6	34.5 – 39.4	36.2	±1.8	5.0
Length Left M1	8	27.0 – 29.0	28.0	±0.7	2.5
Length Right M1	8	26.5 – 29.0	27.9	±0.8	3.0
Width Left M1	9	27.2 – 29.9	28.5	±0.9	3.2
Width Right M1	5	27.0 – 30.0	28.5	±1.2	4.1
Length Left P4	8	18.0 – 19.5	18.7	±0.7	3.5
Length Right P4	6	17.5 – 20.5	18.4	±1.2	6.3
Width Left P4	8	22.7 – 26.0	24.3	±1.2	4.8
Width Right P4	7	22.7 – 26.4	24.6	±1.4	5.8
Length Left P3	7	15.5 – 17.0	16.2	±0.6	3.5
Length Right P3	7	15.5 – 17.0	16.3	±0.5	3.2
Width Left P3	6	18.5 – 20.6	19.7	±0.8	4.1
Width Right P3	5	18.8 – 21.3	20.2	±1.1	5.3
Length Left P2	6	13.0 – 14.5	13.7	±0.5	3.8
Length Right P2	8	13.0 – 16.5	14.2	±1.2	8.6
Width Left P2	5	14.2 – 15.5	14.9	±0.6	4.1
Width Right P2	6	13.6 – 16.0	14.9	±0.9	6.0
Buccal-Lingual Width Left Canine	2	20.1 – 22.8	21.4	±1.9	8.9
Buccal-Lingual Width Right Canine	1	22.5 – 22.5	22.5	±0.0	0.0
Mesial-Distal Width Left Canine	2	21.5 – 24.4	23.0	±2.1	8.9
Mesial-Distal Width Right Canine	1	23.1 – 23.1	23.1	±0.0	0.0
AVERAGE V					4.9[b]

[a] Based, whenever possible, on an average of left and right measurements. [b] Excluding Diastema Length and variables where n=1.

The summary statistics for the smaller-size group (Table 11), however, tend to indicate that there is less variation in this group than is normally encountered in a single extant mammalian species. Although over half of the individual values of V are within the range of a single species, a rather large fraction (over one quarter) are below 4. Most of the values of V that are below 4 were calculated from samples of reasonably large size (n > 5), suggesting that the values of V reflect most of the variation that is actually present. The average value of

V for the smaller-size group (= 6.4) is well within the established range of a single species. Once again canine size may be influencing this result and it will be noted that the values of V for canine size within the smaller-size group are relatively high. If canine size is excluded from the calculation of the average, however, the average value of V for the sample remains within the range of a single species (= 5.6).

TABLE 11. Summary statistics for the small-size group of *Palaeosyops* from Bridger B (all measurements in millimeters).

	n	Range	M	s	V
Basilar Length Skull[a]	1	406.0 – 406.0	406.0	±0.0	0.0
Length Cheek Tooth Series[a]	3	148.0 – 155.0	151.0	±3.6	2.4
Length P2 to M3[a]	4	132.3 – 144.8	139.4	±5.5	3.9
Length Premolar Series[a]	5	51.0 – 67.5	62.0	±6.6	10.6
Length Molar Series[a]	8	86.0 – 98.5	89.6	±4.0	4.5
Length Diastema[a]	3	4.6 – 8.2	6.5	±1.8	28.3
Length Left M3	6	30.5 – 35.5	32.8	±1.8	5.5
Length Right M3	8	31.0 – 34.0	32.5	±1.2	3.8
Width Left M3	6	32.8 – 36.2	34.4	±1.2	3.6
Width Right M3	6	33.0 – 36.1	34.3	±1.2	3.5
Length Left M2	5	31.0 – 33.5	32.1	±1.3	4.0
Length Right M2	7	30.5 – 33.0	31.4	±0.8	2.6
Width Left M2	6	30.7 – 33.6	32.5	±1.1	3.2
Width Right M2	5	30.0 – 33.6	32.2	±1.4	4.2
Length Left M1	4	25.0 – 26.0	25.5	±0.6	2.3
Length Right M1	8	23.5 – 25.0	24.4	±0.6	2.6
Width Left M1	4	25.3 – 25.9	25.6	±0.4	1.4
Width Right M1	7	25.3 – 27.6	26.2	±0.8	2.9
Length Left P4	5	16.9 – 19.0	17.9	±0.9	5.2
Length Right P4	6	16.5 – 19.0	17.4	±0.9	5.3
Width Left P4	5	21.7 – 24.5	23.3	±1.3	5.5
Width Right P4	6	22.5 – 24.4	23.2	±0.7	2.8
Length Left P3	3	15.0 – 17.5	16.2	±1.3	7.8
Length Right P3	6	13.0 – 17.0	15.2	±1.3	8.7
Width Left P3	3	17.4 – 20.0	18.7	±1.3	7.1
Width Right P3	4	17.9 – 20.1	18.9	±1.0	5.5
Length Left P2	3	12.0 – 16.5	14.2	±2.3	15.9
Length Right P2	3	11.0 – 17.0	14.0	±3.0	21.4
Width Left P2	2	14.1 – 15.0	14.5	±0.6	4.4
Width Right P2	2	13.2 – 14.4	13.8	±0.9	6.2
Buccal-Lingual Width Left Canine	2	17.5 – 22.9	20.2	±3.8	19.0
Buccal-Lingual Width Right Canine	0	——	——	±——	——
Mesial-Distal Width Left Canine	2	19.4 – 24.0	21.7	±3.4	15.0
Mesial-Distal Width Right Canine	0	——	——	±——	——
AVERAGE V					6.4[b]

[a] Based, whenever possible, on an average of left and right measurements. [b] Excluding Diastema Length and variables where n=1.

The preceding statistical analyses suggest that there are at least two size groups present within the Bridger B sample. It cannot be determined from these analyses, however, whether these groups represent different species or size groups within a single species (perhaps males and females). Inspection of the specimens in the sample failed to show which of these two possibilities is correct. Although dental material is well preserved in the sample, skulls are in generally poor condition. In most cases it was not possible to determine the sex of the specimens based on the morphology of the temporal crests (see Mader 1989). I also found no morphological characters (cranial or dental) that could be used to define the size groups suggested by the cluster dendrogram in Figure 13 as separate species.
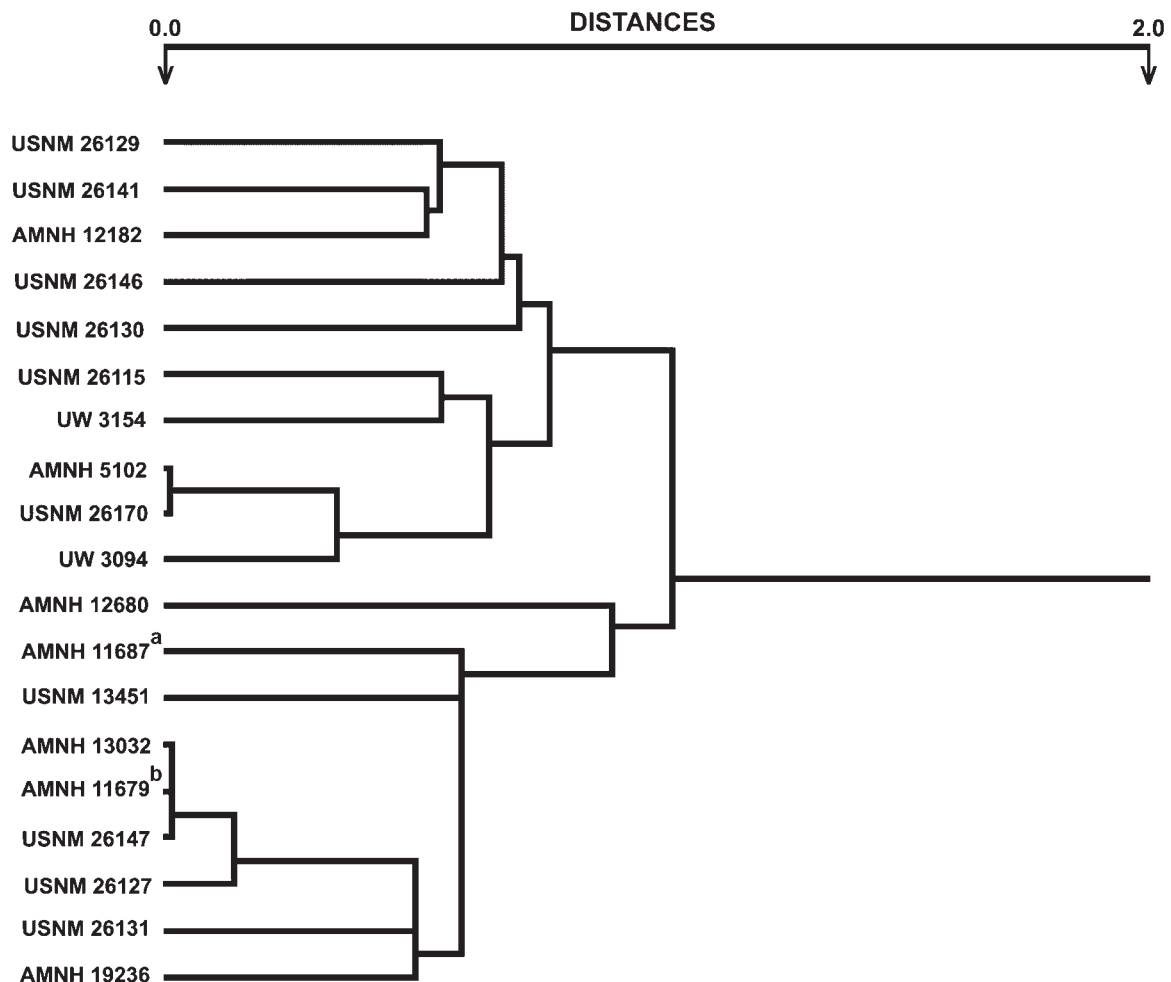

FIGURE 13. Cluster dendrogram for specimens of *Palaeosyops* from Bridger B resulting from a cluster analysis of the length and width of the first upper molars. **a**, type of *Limnohyops priscus*; **b**, type of *Limnohyops monoconus*.

The molar dimensions between the two size groups seem to show a significant difference, which could be an adaptive distinction implying that they are different taxa. However, the size difference between the two groups is actually quite minor (both groups join on the dendrogram at a distance of only one millimeter) and although all *t*-tests that involve molar measurements (see above) show a significant size difference, there is a 54% chance that at least one of these fifteen positive *t*-tests is invalid due to a Type I error. Furthermore, if all *t*-tests performed for this analysis are considered (thirty-one tests), then there is an 80% chance that at least one positive result is in error.

Although it is possible that more than one species may be present in the Bridger B sample, the preceding morphological and statistical analysis did not clearly establish this to be the case. While Osborn (1929) identified several species of *Palaeosyops* (assigned both to *Palaeosyops* and *Limnohyops*) from Bridger B, none of the characters that he used are adequate for diagnostic purposes. In the absence of convincing statistical and morphological evidence for more than a single species I have chosen to take a conservative

approach and recognize only one. The type species of *Palaeosyops*, *P. paludosus*, is from Bridger B and I tentatively assign all specimens from this level to this taxon. Gunnell and Yarborough (2000) recognized a second valid species from this level (*P. laevidens*), which I regard as a junior synonym of *P. paludosus* (see Discussion section for the species *P. paludosus*). If later research should show that more than a single species is actually present in Bridger B then there may be some difficulty in establishing which specimens should be referred to *P. paludosus*. The lectotype of *P. paludosus* is an isolated m2 and may not be adequate for diagnostic purposes. The name *P. paludosus* might have to be regarded as a nomen dubium, therefore.

TABLE 12. F-Test comparisons for *Palaeosyops* from Bridger B (Group 1) and Bridger C (Group 2).

	n Group 1	n Group 2	F	Probability	*T*-Test
Basilar Length Skull[a]	4	1	———	———	———[b]
Length Cheek Tooth Series[a]	8	3	2.595	0.111	Pooled
Length P2 to M3[a]	12	4	0.384	0.536	Pooled
Length Premolar Series[a]	11	4	0.817	0.367	Pooled
Length Molar Series[a]	17	4	0.692	0.406	Pooled
Length Diastema[a]	9	2	0.161	0.691	Pooled
Length Left M3	17	7	0.588	0.443	Pooled
Length Right M3	19	7	0.105	0.746	Pooled
Width Left M3	15	4	0.128	0.721	Pooled
Width Right M3	17	7	0.206	0.650	Pooled
Length Left M2	15	7	1.490	0.222	Pooled
Length Right M2	16	8	0.375	0.540	Pooled
Width Left M2	15	3	0.131	0.718	Pooled
Width Right M2	13	5	0.252	0.616	Pooled
Length Left M1	12	4	0.002	0.961	Pooled
Length Right M1	16	6	0.022	0.882	Pooled
Width Left M1	13	3	0.457	0.501	Pooled
Width Right M1	12	5	0.535	0.465	Pooled
Length Left P4	14	4	0.017	0.896	Pooled
Length Right P4	14	7	4.347	0.037	Separate
Width Left P4	15	4	2.368	0.125	Pooled
Width Right P4	14	6	7.659	0.006	Separate
Length Left P3	12	3	———	———	———[b]
Length Right P3	15	6	2.979	0.084	Pooled
Width Left P3	10	4	1.714	0.192	Pooled
Width Right P3	11	6	2.738	0.099	Pooled
Length Left P2	11	3	2.385	0.126	Pooled
Length Right P2	13	4	0.465	0.496	Pooled
Width Left P2	9	3	0.867	0.354	Pooled
Width Right P2	8	4	2.155	0.144	Pooled
Buccal-Lingual Width Left Canine	5	2	0.197	0.661	Pooled
Buccal-Lingual Width Right Canine	2	1	———	———	———[b]
Mesial-Distal Width Left Canine	5	2	0.256	0.618	Pooled
Mesial-Distal Width Right Canine	2	1	———	———	———[b]

[a] Based, whenever possible, on an average of left and right measurements. [b] There is no variance in one of the two groups being compared.

TABLE 13. *T*-Test comparisons for *Palaeosyops* from Bridger B and Bridger C.

	T	DF	Probability
Basilar Length Skull[a]	——[b]	——	——
Length Cheek Tooth Series[a]	2.473	9.0	0.035
Length P2 to M3[a]	2.630	14.0	0.020
Length Premolar Series[a]	1.624	13.0	0.128
Length Molar Series[a]	3.238	19.0	0.004
Length Diastema[a]	0.152	9.0	0.882
Length Left M3	4.152	22.0	0.000
Length Right M3	4.227	24.0	0.000
Width Left M3	3.343	17.0	0.004
Width Right M3	3.165	22.0	0.004
Length Left M2	2.570	20.0	0.018
Length Right M2	1.779	22.0	0.089
Width Left M2	1.720	16.0	0.105
Width Right M2	0.876	16.0	0.394
Length Left M1	2.380	14.0	0.032
Length Right M1	3.333	20.0	0.003
Width Left M1	3.189	14.0	0.007
Width Right M1	4.385	15.0	0.001
Length Left P4	1.062	16.0	0.304
Length Right P4	1.118[c]	7.5	0.300
Width Left P4	1.651	17.0	0.117
Width Right P4	0.915[c]	5.6	0.402
Length Left P3	——[b]	——	——
Length Right P3	1.554	19.0	0.137
Width Left P3	0.138	12.0	0.892
Width Right P3	0.975	15.0	0.345
Length Left P2	0.854	12.0	0.410
Length Right P2	1.574	15.0	0.136
Width Left P2	0.072	10.0	0.944
Width Right P2	2.335	10.0	0.042
Buccal-Lingual Width Left Canine	0.700	5.0	0.515
Buccal-Lingual Width Right Canine	——[b]	——	——
Mesial-Distal Width Left Canine	0.786	5.0	0.468
Mesial-Distal Width Right Canine	——[b]	——	——

[a] Based, whenever possible, on an average of left and right measurements. [b] Insufficient data for *t*-test. c Separate *t*-test.

The Twin Buttes Member of the Bridger Formation is divisible into two stratigraphic levels: Bridger C and Bridger D. Although it would have been desirable to perform *t*-test comparisons to determine whether the samples from Bridger C and D are significantly different in size, the sample from Bridger D is rather small (four individuals), making this impractical. *T*-tests (Tables 12 and 13) suggest, however, that there is a significant difference in molar size between specimens of *Palaeosyops* from Bridger C and from Bridger B (Blacks Fork Member of the Bridger Formation). Eighty percent of measurements that involve the molars

(length of cheek tooth series, length of cheek tooth series exclusive of P1, length of molar series, and length and width of individual molars) test as significantly different (only the length of the right M2 and width of both M2's do not). Among those *t*-tests that concern measurements involving the molars there is a 54% chance that at least one of these significant results is invalid due to a Type I error. Among all thirty *t*-tests performed for this analysis there is a 79% chance that at least one of the significant results is an invalid rejection of the null hypothesis.

TABLE 14. Summary statistics for *Palaeosyops* from Bridger C (all measurements in millimeters).

	n	Range	M	s	V
Basilar Length Skull[a]	1	405.5 – 405.5	405.5	±0.0	0.0
Length Cheek Tooth Series[a]	3	165.0 – 169.5	167.7	±2.4	1.4
Length P2 to M3[a]	4	151.5 – 165.0	156.5	±6.3	4.0
Length Premolar Series[a]	4	65.3 – 72.0	67.7	±3.1	4.6
Length Molar Series[a]	4	98.5 – 107.5	102.5	±3.8	3.7
Length Diastema[a]	2	6.0 – 8.0	7.0	±1.4	20.5
Length Left M3	7	35.5 – 40.0	37.5	±1.5	4.1
Length Right M3	7	34.0 – 42.5	38.1	±2.8	7.3
Width Left M3	4	37.3 – 43.1	40.3	±2.7	6.6
Width Right M3	7	37.1 – 42.5	39.4	±2.3	5.8
Length Left M2	7	33.5 – 41.5	36.0	±2.8	7.7
Length Right M2	8	30.0 – 38.5	34.4	±2.6	7.6
Width Left M2	3	35.4 – 40.3	37.2	±2.7	7.2
Width Right M2	5	34.9 – 40.1	36.1	±2.2	6.1
Length Left M1	4	27.5 – 31.0	29.1	±1.4	4.9
Length Right M1	6	27.0 – 31.5	29.2	±1.8	6.2
Width Left M1	3	29.6 – 33.8	31.2	±2.3	7.4
Width Right M1	5	29.1 – 33.3	31.0	±2.0	6.5
Length Left P4	4	18.0 – 20.0	18.9	±0.9	4.5
Length Right P4	7	14.5 – 22.0	18.8	±2.4	12.8
Width Left P4	4	24.4 – 25.9	25.0	±0.6	2.5
Width Right P4	6	19.8 – 30.7	25.4	±3.6	14.0
Length Left P3	3	17.0 – 17.0	17.0	±0.0	0.0
Length Right P3	6	13.5 – 18.5	16.8	±1.9	11.2
Width Left P3	4	16.5 – 20.7	19.4	±2.0	10.3
Width Right P3	6	16.0 – 22.6	20.5	±2.4	11.7
Length Left P2	3	12.5 – 17.5	14.7	±2.6	17.5
Length Right P2	4	14.5 – 17.0	15.4	±1.1	7.2
Width Left P2	3	13.0 – 16.2	14.8	±1.7	11.2
Width Right P2	4	15.4 – 16.2	15.8	±0.4	2.6
Buccal-Lingual Width Left Canine	2	20.7 – 22.8	21.8	±1.5	6.8
Buccal-Lingual Width Right Canine	1	20.4 – 20.4	20.4	±0.0	0.0
Mesial-Distal Width Left Canine	2	20.0 – 21.7	20.8	±1.2	5.9
Mesial-Distal Width Right Canine	1	21.2 – 21.2	21.2	±0.0	0.0
AVERAGE V					7.0[b]

[a] Based, whenever possible, on an average of left and right measurements. [b] Excluding Diastema Length and variables where n=1.
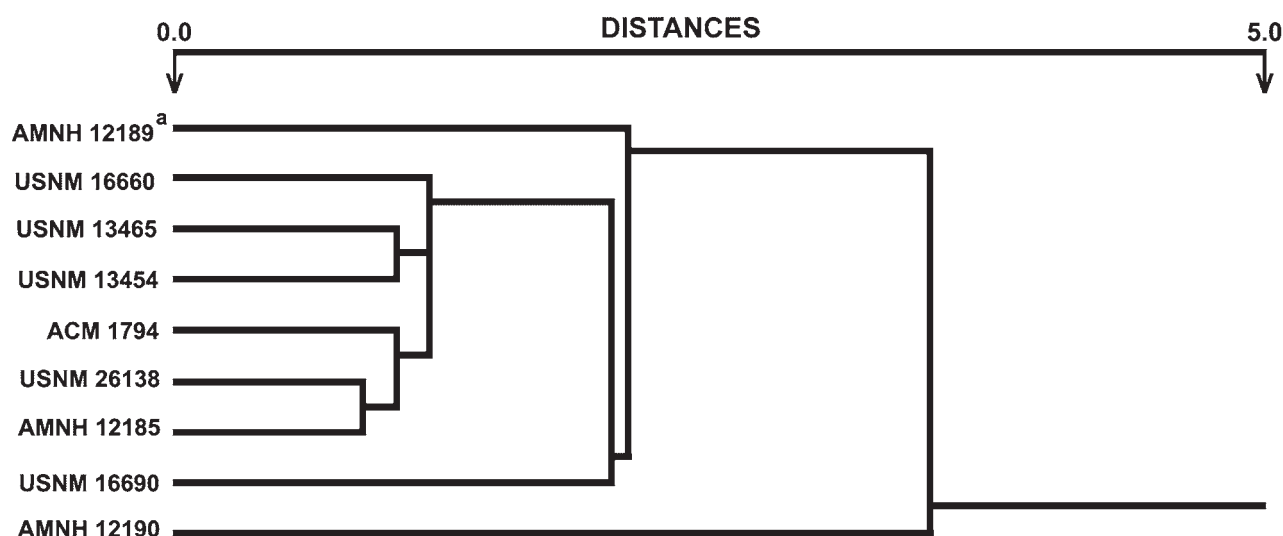
FIGURE 14. Cluster dendrogram for specimens of *Palaeosyops* from Bridger C resulting from a cluster analysis of all variables listed in Table 14. **a**, type of *P. grangeri*.

The summary statistics for the Bridger C sample are presented in Table 14. In this table almost two-thirds of the individual values of V are within the accepted range for a single species. A number of premolar measurements, however, have values of V greater than 10, and the average value of V for the sample is also rather high (= 7.0) although within the accepted range of a single species.

Cluster analyses of all of the variables listed in Table 14 results in the dendrogram illustrated in Figure 14. Most specimens on this dendrogram (ACM 1794, AMNH 12185, USNM 13454, USNM 13465, USNM 16660, and USNM 26138) are distributed in an essentially homogeneous fashion, clustering together at a distance of 1.2 millimeters. Three specimens, however, join this cluster at slightly further distances. USNM 16690 and AMNH 12189 join at 2.0 and 2.1 millimeters respectively, and AMNH 12190 joins at a distance of 3.5 millimeters.

Although the groupings in this cluster dendrogram are not completely homogeneous, there is no clear delineation into size groups. Cluster analysis of various combinations of the characters listed in Table 14 also failed to differentiate size groups. Although some of the individual values of V are rather high in the Bridger C sample, there is not enough evidence to justify the recognition of more than a single species from this stratigraphic level. Specimens of *Palaeosyops* from Bridger C are apparently distinguished from specimens of *Palaeosyops* from Bridger B by their larger size (especially the molars) although there is considerable size overlap. Based upon this difference, I provisionally recognize the species of *Palaeosyops* from Bridger C as being taxonomically distinct from *P. paludosus* in Bridger B. The earliest new name to be assigned to a specimen of *Palaeosyops* clearly recorded from Bridger C is *Palaeosyops robustus* (Marsh 1872), and I tentatively refer all specimens of *Palaeosyops* from this level to that species (see Discussion for *P. robustus* below).

The sample of *Palaeosyops* from Bridger D is too small to analyze separately. Table 15, however, presents the summary statistics for specimens of *Palaeosyops* from the entire Twin Buttes Member of the Bridger Formation including both Bridger C and D. As shown by this table, most of the individual values of V are within the range established for a single species, as is the average value of V for the sample. Only a small fraction of the individual values of V are less than 4 or greater than 10. This result suggests that the sample of *Palaeosyops* from the Twin Buttes Member of the Bridger Formation is essentially homogeneous and there is no indication that more than a single species is present. I provisionally refer all of the *Palaeosyops* material from Bridger D, therefore, to *P. robustus*.

TABLE 15. Summary statistics for *Palaeosyops* from the Twin Buttes Member of the Bridger Formation (all measurements in millimeters).

	n	Range	M	s	V
Basilar Length Skull[a]	1	405.5 – 405.5	405.5	±0.0	0.0
Length Cheek Tooth Series[a]	3	165.0 – 169.5	167.7	±2.4	1.4
Length P2 to M3[a]	5	151.5 – 165.0	155.8	±5.7	3.6
Length Premolar Series[a]	5	65.3 – 72.0	67.7	±2.7	4.0
Length Molar Series[a]	6	98.5 – 107.5	101.5	±3.3	3.3
Length Diastema[a]	3	6.0 – 8.0	6.7	±1.2	17.5
Length Left M3	10	35.5 – 40.0	37.0	±1.5	4.0
Length Right M3	9	34.0 – 42.5	37.9	±2.5	6.6
Width Left M3	8	36.5 – 43.1	39.3	±2.3	5.9
Width Right M3	9	37.1 – 42.5	39.5	±2.0	5.0
Length Left M2	12	33.0 – 41.5	35.4	±2.3	6.3
Length Right M2	13	30.0 – 38.5	34.9	±2.2	6.2
Width Left M2	9	34.3 – 40.3	36.4	±2.0	5.4
Width Right M2	8	34.6 – 40.1	36.0	±1.9	5.3
Length Left M1	9	27.0 – 31.0	28.7	±1.2	4.3
Length Right M1	8	27.0 – 31.5	28.9	±1.6	5.7
Width Left M1	8	28.6 – 33.8	30.1	±1.6	5.4
Width Right M1	6	28.6 – 33.3	30.6	±2.0	6.7
Length Left P4	9	18.0 – 20.0	18.7	±0.6	3.3
Length Right P4	11	14.5 – 22.0	18.7	±2.0	10.6
Width Left P4	9	23.5 – 26.0	24.8	±0.9	3.4
Width Right P4	8	19.8 – 30.7	25.6	±3.1	12.0
Length Left P3	7	17.0 – 17.0	17.0	±0.0	0.0
Length Right P3	10	13.5 – 18.5	16.8	±1.5	8.9
Width Left P3	9	16.5 – 21.9	20.2	±1.5	7.6
Width Right P3	8	16.0 – 22.6	20.6	±2.1	10.1
Length Left P2	7	12.5 – 17.5	14.9	±1.6	10.5
Length Right P2	9	13.0 – 17.0	14.8	±1.1	7.4
Width Left P2	7	13.0 – 17.8	15.7	±1.7	10.6
Width Right P2	5	15.2 – 16.2	15.7	±0.4	2.8
Buccal-Lingual Width Left Canine	2	20.7 – 22.8	21.8	±1.5	6.8
Buccal-Lingual Width Right Canine	1	20.4 – 20.4	20.4	±0.0	0.0
Mesial-Distal Width Left Canine	2	20.0 – 21.7	20.8	±1.2	5.9
Mesial-Distal Width Right Canine	1	21.2 – 21.2	21.2	±0.0	0.0
AVERAGE V					6.0[b]

[a] Based, whenever possible, on an average of left and right measurements. [b] Excluding Diastema Length and variables where n=1.

Species *Palaeosyops paludosus* Leidy 1870

= *P. major* Leidy 1871
= *P. minor* Marsh 1871a?
= *P. montanus* (Marsh 1871b)
= *P. humilis* Leidy 1872a
= *P. laevidens* Cope 1872
= *P. longirostris* Earle 1892
= *P. priscus* (Osborn 1908)
= *P. matthewi* (Osborn 1908)
= *P. monoconus* (Osborn 1908)

Lectotype: USNM 759, a lower second molar.

Referred specimens: AMNH 1561, AMNH 5102, AMNH 5104 (lectotype of *Palaeosyops laevidens*), AMNH 11679 (type of *Limnohyops monoconus*), AMNH 11684 (type of *Limnohyops matthewi*), AMNH 11687 (type of *Limnohyops priscus*), AMNH 12182, AMNH 12680, AMNH 13032, AMNH 19236, USNM 13451, USNM 26115, USNM 26117, USNM 26127, USNM 26129, USNM 26130, USNM 26131, USNM 26132, USNM 26141, USNM 26146, USNM 26147, USNM 26170, UW 3094, UW 3154, YPM 11137.

Diagnosis: Species of *Palaeosyops* intermediate in size between *P. fontinalis* and *P. robustus* (length P2 to M3 is approximately 129 to 161 mm).

Discussion: The correct name holder for this species is USNM 759, the lectotype selected by Osborn (1929). Osborn (1929) also designated a lower jaw (AMNH 11680) as a "neotype" for the species but, because the original type is still preserved, this jaw has no nomenclatural significance and is merely a referred specimen (Article 75, International Code of Zoological Nomenclature, Ride *et al.* 1999). Similarly, the skull, jaw, and postcranials (UM 98890) that Gunnell and Yarborough (2000) designated as a "neotype" of *P. paludosus* cannot be recognized as the name holder under the provisions of the International Code.

As indicated above in the Discussion section for the genus *Palaeosyops*, all of the *Palaeosyops* material from Bridger B is provisionally referred to the species *P. paludosus*. At present *P. paludosus* is poorly distinguished from both *P. fontinalis* and *P. robustus*. As a group, specimens of *P. paludosus* are intermediate in size between specimens of *P. fontinalis* and *P. robustus* but there is considerable size overlap. Thus, large specimens of *P. fontinalis* equal or exceed the size of smaller specimens of *P. paludosus* and large specimens of *P. paludosus* equal or exceed the size of small specimens of *P. robustus*.

One year after Leidy described the type of *Palaeosyops paludosus* he named a new species of *Palaeosyops*, *P. major*, based on a pathologic lower jaw (ANSP 10421) lacking all of the dentition (Leidy 1871). In 1929, Osborn designated a "neotype" skull (AMNH 12182) and jaw (AMNH 12181) for this species, but once again the original type is still preserved and Osborn's skull and jaw are simply referred specimens. The type of *P. major* is identifiable as a specimen of *Palaeosyops* but is virtually useless as a type. If at some future date more than one species of *Palaeosyops* should be recognized in Bridger B, then *P. major* would probably have to be regarded as a nomen dubium.

In the same year, Marsh (1871a) described a right lower molar from Grizzly Buttes, which he identified as a new species of *Palaeosyops*, *P. minor*. I have not had the opportunity to examine this specimen, but assuming that Marsh was correct in identifying it as a brontothere, then it should be referred to *P. paludosus* since this is the only brontothere species that I recognize from this geologic level (Blacks Fork Member of Bridger Formation). Thus I tentatively regard *P. minor* as a junior synonym of *P. paludosus*. *Palaeosyops minor* Marsh is a primary senior homonym of *P. minor* Earle (1891), which Osborn (1929) also referred to *P. paludosus*. As a junior homonym, the name *P. minor* Earle is invalid (Article 57.2, International Code of Zoological Nomenclature, Ride *et al.* 1999).

Marsh (1871b) described teeth and parts of a postcranial skeleton, which he identified as a new species of carnivore, *Canis montanus*. Of this material Osborn selected a second lower premolar (misidentified by Marsh as a last upper premolar) as a lectotype for the species and correctly recognized that it is a specimen of *Palaeosyops*. Once again, the locality (Grizzly Buttes) places the specimens in the Blacks Fork Member of the Bridger Formation and, thus, I recognize *P. montanus* as a junior synonym of *P. paludosus*.

In 1872 Leidy described a small tooth from "Dry Creek Canyon" forty miles (64 km) from Fort Bridger, Wyoming, which he identified as a new species of *Palaeosyops*, *P. humilis* (Leidy 1872a). At first Leidy identified this tooth as a molar, but later correctly recognized that it is actually a deciduous premolar. Osborn (1929) suggested that this specimen is from Bridger C, and if this is the case, then it should be referred to *P. robustus*. The locality description, however, suggests to me that the specimen is probably from exposures of Bridger B along either Dry Creek or Little Dry Creek forty miles (64 km) west of Fort Bridger (see map of the Green River Basin in West 1976).

In 1872 Cope also named a new species of *Palaeosyops*, *P. laevidens*, based on two cotypes. One specimen, AMNH 5104, was from Cottonwood Creek in the Green River Basin and the other specimen, AMNH 5105, was from Bitter Creek in the Washakie Basin. Because Cope (1885) "selects, describes, and figures" AMNH 5104 as the "type", Osborn (1929) recognized this specimen as the lectotype of the species. AMNH 5104 is from Bridger horizon B and is referred, therefore, to *P. paludosus* in the present paper.

In 1892 Earle named a new species of *Palaeosyops*, *P. longirostris*, based on a partial jaw (YPM-PU 10275) from Cottonwood Creek in the Green River Basin. The trivial name was in allusion to the supposedly great posterior extension of the lower jaw behind the last molar. Unfortunately, much of the type specimen may be lost. I have only been able to locate two fragments of the specimen and could find none of the teeth. Since deposits along Cottonwood Creek belong to Bridger B, I refer this specimen to *P. paludosus*.

Osborn (1908) named three new species of "*Limnohyops*" from Bridger B the types of which were all collected from Grizzly Buttes. "*Limnohyops*" *priscus* was based on a severely deformed skull (AMNH 11687) with well-preserved dentition. In 1929 Osborn provided a "partial reconstruction" of this specimen (1929, Fig. 259) that is mostly imaginary. The specimen is almost crushed flat and very little of the cranial morphology can be observed.

"*Limnohyops*" *matthewi* was based on the posterior part of a skull (AMNH 11684), but most of the characters that Osborn (1908; 1929) used to define the taxon (high and narrow occiput, postglenoid and post-tympanic processes in close contact, and shape of the temporal fossae) are actually the result of taphonomic deformation in the type.

"*Limnohyops*" *monoconus* was based on a fragmentary skull (AMNH 11679) and was distinguished from other specimens of "*Limnohyops*" by the absence of the hypocone on M3.

Palaeosyops paludosus is the only species of *Palaeosyops* from Bridger B that I recognize as valid, although cluster analysis does suggest more than a single size group is present (see Discussion section for the genus *Palaeosyops*). Gunnell and Yarborough (2000) recognized a second valid species from this level: *P. laevidens* (here a junior synonym of *P. paludosus*). Specimens assigned by Gunnell and Yarborough to *P. paludosus* and *P. laevidens* do not correspond to the size groups delineated in Figures 12 and 13.

According to Gunnell and Yarborough (2000) *Palaeosyops paludosus* is larger in size (especially the premolars and first molar) than *P. laevidens* and has more molarized premolars. My impression, however, is that the premolar morphology is not discretely different among specimens that they place in the two species and most premolar and molar size ranges overlap (based on their published data). Given that the coefficient of variation for all specimens from Bridger B falls within the range of a single extant mammalian species (see Discussion section for the genus *Palaeosyops*), *P. paludosus* and *P. laevidens* should probably be regarded as synonyms.

Species *Palaeosyops fontinalis* (Cope 1873a)

= *P. huerfanensis* (Osborn 1919)

Holotype: AMNH 5107, a fragmentary juvenile skull with the right DP4 and M1–2 preserved.
   Referred specimens: AMNH 17411, AMNH 17412 (type of *P. huerfanensis*), AMNH 17425, UW 3039, UW3091.
   Diagnosis: Small-sized species of *Palaeosyops* (based on AMNH 17411, UW 3039, and UW 3091, length of P2 to M3 is approximately 123 to 144 mm) that may be distinguished from *P. paludosus* and *P. robustus* by

its smaller size and perhaps by the more plesiomorphic structure of P2 and relatively small fronto-parietal dome.

Discussion: As indicated in the Discussion section for the genus *Palaeosyops*, I provisionally recognize specimens of *Palaeosyops* from Bridger A as being taxonomically distinct from *P. paludosus* from Bridger B. The size range of *P. fontinalis* overlaps with that of *P. paludosus*, however, and the P2 in one specimen referred to *P. fontinalis* (UW 3039) is not as plesiomorphic as that of UW 3091. The type of *P. fontinalis* is from Bridger A, and I tentatively refer all of the *Palaeosyops* material from this level to that species. Additional statistical and morphological analysis will be required to confirm whether *P. fontinalis* is valid and, if valid, whether all of the material from Bridger A can be referred to this taxon.

I also tentatively refer specimens of *Palaeosyops* from the Huerfano Formation to *P. fontinalis* because of their relatively small size and because there is no basis at present for distinguishing them from specimens of *Palaeosyops* from Bridger A. Assignment of the Huerfano specimens to *P. fontinalis* must be regarded as very uncertain, however, until more material is available for examination. As noted in the Discussion section for the genus *Palaeosyops*, above, if it should later prove that the Huerfano specimens represent a distinct species, then the name *P. huerfanensis* (Osborn) may apply.

Species *Palaeosyops robustus* (Marsh 1872)

= *P. laticeps* Marsh 1872
= *P. diaconus* Cope 1873b
= *P. leidyi* Osborn 1908
= *P. grangeri* Osborn 1908
= *P. copei* Osborn 1908

Holotype: YPM 11122, a fragmentary skull.

Referred specimens: ACM 1794, AMNH 1544 (type of *P. leidyi*), AMNH 1554, AMNH 1558, AMNH 1580, AMNH 2361, AMNH 5105, AMNH 5106 (type of *P. diaconus*), AMNH 11678, AMNH 11683, AMNH 11708 (type of *P. copei*), AMNH 11710, AMNH 12185, AMNH 12189 (type of *P. grangeri*), AMNH 12190, UCM 19489, USNM 6704, USNM 12694, USNM 13454, USNM 13464, USNM 13465, USNM 13466, USNM 16660, USNM 16661, USNM 16690, USNM 26120, USNM 26138, YPM 11000 (tentatively included, type of *P. laticeps*), YPM 11150, YPM-PU 10009.

Diagnosis: Species of *Palaeosyops* distinguished from *P. fontinalis* and *P. paludosus* by its larger size (length P2 to M3 is approximately 150 to 165 mm).

Discussion: As indicated in the Discussion section for the genus *Palaeosyops*, I recognize only a single valid species of *Palaeosyops* from the Twin Buttes Member of the Bridger Formation (Bridger C and D). Because "*Limnohyus*" *robustus* Marsh (1872) is the first species of *Palaeosyops* that is based on a type reliably known to have been collected from this level I have referred all specimens of *Palaeosyops* from the Twin Buttes Member of the Bridger Formation to this taxon.

In the same paper, however, Marsh (1872) also described another new species of *Palaeosyops*, which he named *P. laticeps*. This specimen was recorded from "Marsh's Fork", approximately fifteen miles (24 km) from Fort Bridger. Although there are several creeks located ten to fifteen miles (16–24 km) southwest of Fort Bridger, there is no creek known as "Marsh's Fork". It is not certain, therefore, which stratigraphic horizon this specimen is from, but if it was collected in the vicinity of Cottonwood Creek or Black's Fork, then it is probably from Bridger B (Blacks Fork Member). However, if the distance is accurately recorded as fifteen miles (24 km), then the locality would almost certainly be in the Twin Buttes Member. The Sage Creek White Layer, which is the boundary between Bridger B (Blacks Fork Member) and Bridger C (Twin Buttes Member) is found in deposits located approximately eleven to twelve miles (18–19 km) from Fort Bridger. Because of the uncertainty of the stratigraphic level I only tentatively regard *P. laticeps* as a synonym of *P. robustus*.

In accordance with the Principle of First Reviser (Article 24.2.1, International Code of Zoological Nomenclature, Ride *et al*. 1999) I select the name *Palaeosyops robustus* as having priority over the name *P.*

laticeps, as this will best serve nomenclatural stability (Recommendation 24A), because the stratigraphic level from which the type of *P. laticeps* was collected is uncertain and *P. laticeps* could thus be a junior synonym of *P. paludosus* from Bridger B. It should be noted that Marsh discussed *Palaeosyops laticeps* before he discussed "*Limnohyus*" *robustus* in his 1872 paper, but the International Code does not recognize the concept of "page priority" (Nemésio 2007).

Specimens of *Palaeosyops* from the Adobe Town Member of the Washakie Formation, which is chronologically equivalent to the Twin Buttes Member of the Bridger Formation, are also referred to *P. robustus*. Because of the small sample size of *Palaeosyops* from the Washakie Formation (n=4) statistical analysis of the sample is not practical at this time.

In the same year that Marsh described "*Limnohyus*" *robustus*, Leidy (1872a) described the type of *P. humilis*, which Osborn (1929) alleged to be from Bridger C. As indicated in the discussion for the species *P. paludosus*, however, this specimen is probably from Bridger B and is thus referred to *P. paludosus*.

In 1873 Cope described parts of two maxillae with some of the cheek dentition preserved (AMNH 5106), which he identified as a new species of *Palaeosyops*, *P. diaconus* (Cope 1873b). This specimen is from Henry's Fork and is thus from the Twin Buttes Member of the Bridger Formation and represents *P. robustus*.

In 1908, Osborn described three new species of *Palaeosyops*, all of which I refer to *P. robustus*. *Palaeosyops leidyi* was based on a well-preserved skull (AMNH 1544) from Henry's Fork; P. *grangeri* was based on a palate from Twin Buttes with the grinding teeth and parts of the lower jaw and skull preserved (AMNH 12189); and *P. copei* was based on a series of upper grinding teeth (AMNH 11708) from Henry's Fork at Lone Tree.

In addition to *Palaeosyops robustus*, Gunnell and Yarborough (2000) recognized a second valid species of *Palaeosyops* from Bridger C: *P. laticeps* (here regarded as a synonym of *P. robustus*). Gunnell and Yarborough distinguished *P. laticeps* from *P. robustus* by the former's smaller size (especially in upper premolar dimensions) and relatively distinct hypocones on M3. However, specimens that Gunnell and Yarborough assign to the two species overlap in size for many variables (based on their published data). Furthermore, as indicated above, the distal part of the brontothere tooth row is highly variable and the size and morphology of the M3 hypocone generally makes a poor diagnostic character. Thus, the weight of evidence suggests that there is a single species of *Palaeosyops* in the Twin Buttes Member of the Bridger Formation and its stratigraphic equivalents.

Conclusion

Eotitanops is the only member of the subfamily Eotitanopinae and *Palaeosyops* is the only member of the subfamily Palaeosyopinae. The present revision recognizes two valid species of *Eotitanops* (*E. borealis* and *E. gregoryi*) and three valid species of *Palaeosyops* (*P. paludosus*, *P. fontinalis*, and *P. robustus*).

Because of to their fragmentary nature, specimens identified as *Eotitanops gregoryi* and specimens from the Huerfano Formation identified as *Palaeosyops fontinalis* cannot be referred to those genera with absolute certainty. Furthermore, statistical analysis suggests that there may be a second species of *Palaeosyops* from Bridger B (upper part of the Blacks Fork Member of the Bridger Formation) in addition to *P. paludosus*, the one species from that level that is recognized here. The evidence for a second species from Bridger B is not compelling, however.

Gunnell and Yarborough (2000) published a revision of the genera *Eotitanops* and *Palaeosyops* with conclusions similar to the present paper. Regarding *Eotitanops*, both the present paper and Gunnell and Yarborough recognize a large form and a small form, and both papers refer the large form to *E. borealis*. The present paper refers the small form to *E. gregoryi*, however, while Gunnell and Yarborough referred it to *E. minimus* (here regarded as a junior synonym of *E. gregoryi*). Gunnell and Yarborough regarded *E. gregoryi* as a junior synonym of *E. borealis*.

Concerning the genus *Palaeosyops*, the present paper recognizes three species as valid (*P. fontinalis*, *P. paludosus*, and *P. robustus*), whereas Gunnell and Yarborough accepted five (*P. fontinalis*, *P. paludosus*, *P.*

robustus, *P. laevidens*, and *P. laticeps*). In the present paper *P. laevidens* is regarded as a junior synonym of *P. paludosus* and *P. laticeps* is regarded as a junior synonym of *P. robustus*.

As first reviser I have selected the name *Palaeosyops robustus* as having priority over the name *P. laticeps*, both of which were published in the same paper (Marsh 1872). Even though *P. laticeps* was described first, the International Code does not recognize the concept of "page priority" (wherein the name appearing in a publication first has priority over names appearing later in the same paper if they are found to be synonyms). Following the recommendation of the Code, this choice is intended to best serve nomenclatural stability (see Discussion section for the species *P. robustus*).

Over the years, several invalid neotypes have been designated for species of *Eotitanops* and *Palaeosyops* that have no status as name-holders because the original type specimens are still preserved. These include the "neotypes" of *Eotitanops borealis* (AMNH 14887, Osborn 1929), *Palaeosyops paludosus* (AMNH 11680, Osborn 1929; UM 98890, Gunnell & Yarborough 2000), and *Palaeosyops major* (AMNH 12181 and AMNH 12182, Osborn 1929).

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